THE UNIVERSITY OF ALBERTA

ECOLOGICAL ASPECTS OF FOOD SELECTION IN PINE MARTEN
(*MARTES AMERICANA*)

BY

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Ecological Aspects of Food Selection in Pine Marten (*Martes americana*)" submitted by Gavin More in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

A study of food selection in pine marten (*Martes americana*) was conducted in the southern Northwest Territories (60° 45' N, 116° 37' W) from 1974-75. Marten food habits were derived from an analysis of 501 scats and kills. Mammals were the major food source. Small mammals, notably boreal red-backed voles (*Clethrionomys gapperi*) and meadow voles (*Microtus pennsylvanicus*), were the principal species of marten diet. Red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hares (*Lepus americanus*) were taken infrequently. Deer mice (*Peromyscus maniculatus*) were rarely found in scats, despite their apparent abundance in the study area.

Radio-telemetry techniques were used to study marten habitat use, and activity. Habitats in which marten were located were compared with a sample of randomly selected habitats by means of Multiple Classification Analysis (MCA). Summer, fall and winter habitats that showed greater than expected use were mesic habitats, mostly coniferous and mixed deciduous stands of moderate to high stand density. Very open xeric, and open moist sites showed less than expected use.

Marten had bimodal activity periods in the early morning and evening in summer. These periods of activity were modified in fall and winter. Marten were seldom active between mid-morning and late afternoon in summer and fall but were active during the morning in winter. Changes in circadian rhythms may be attributable to changes in the physical environment such as day length.

Weather influenced marten activity to a variable extent. They tended to be active on overcast or rainy days, and inactive on clear or snowy days.

Much of the observed food selection in marten is explained by the ecological availability of prey. The major ecological spacing mechanisms involved were temporal and spatial overlap of marten and their prey. *C. gapperi* exhibited the most extensive overlap, both temporally and spatially, and occurred most frequently in marten scats. Spatial and temporal overlap was low between *P. maniculatus* and marten thus explaining the low occurrence of this species in marten diet despite their abundance in snap-trap samples.

Marten tended to specialize on small mammals, and obtained most of their food requirements from *C. gapperi* and *M. pennsylvanicus*. When populations of the principal small mammals were below normal or were unavailable, marten preyed on other species. Large male marten killed large species such as *T. hudsonicus* and *L. americanus*. Females and young marten may be unable to kill large prey with adequate success to maintain themselves, and the population of marten subsequently declined.

Marten predation had little impact on *C. gapperi* populations in years of average vole densities. Predation was high during the decline phase of voles in the winter and spring of 1974-75. However, *C. gapperi* numbers recovered to normal by fall 1975. Thus, marten predation cannot be considered a significant factor in microtine fluctuations despite heavy predation during the decline phase.

ACKNOWLEDGEMENTS

The major portion of the field programme was financed by the Canadian Wildlife Service. Radio-telemetry equipment was provided by the Bioelectronics Unit of the Canadian Wildlife Service. Live-traps were borrowed from the Northwest Territories Game Branch. The Heart Lake Biological Station served as a home for 16 months through the auspices of Dr. W. A. Fuller. Other financial support was provided by the Department of Zoology through Graduate Teaching Assistantships and an Intersession Bursary, and the National Research Council of Canada through grants to Dr. W. A. Fuller. I am grateful to Parks Division, Alberta Recreation, Parks and Wildlife for employing me during the final stages of the production of this thesis.

Persons who provided field assistance were numerous. My thanks go to Doug Stewart, Gary Stenson, Rick Sawatsky, Euan McPhee, Steve Mihok, Maggie Ballantyne, Dave Doyle and Gordie Fuller for services rendered, particularly for their collection of marten scats. Dave Doyle identified the shrew teeth in the scats. Euan McPhee helped to supply fodder for the marten during their stay at the Heart Lake Marten Inn.

Nick Novakowski of the Canadian Wildlife Service is responsible for my return to university. Art Martell and Verne Hawley, also of the Canadian Wildlife Service, provided the essential moral support, advice and encouragement when life was at its lowest. Bob Hudson advised in battling the Murphy in the university computer. Special

thanks for exceptional editorial aid are due to Art Martell and Dr. W. A. Fuller for tackling my attempt at the world's most difficult language. Numerous friends and advisors suggested comments and commas including Fred Zwickel, Bob Hudson, and Joanne Robertson. Anne Osadchuk generously typed the final draft.

Finally, I acknowledge my debt to the pine marten; a most gentle, fragile and yet fearless creature.

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INTRODUCTION

One of the most complex problems of predator ecology is that of food selection. Ewer (1973:139) characterized a highly successful carnivore as one having "sufficient specialization to make an effective predator with flexibility to permit a variety of food in relation to changing seasons or varied habitat." Theoretically, fluctuations in prey density favor generalist predators over specialists, when food species vary in a consistent fashion (Schoener 1971). Predators tend to be specialists when prey is abundant but diversify their diet as prey becomes scarce (Emlen 1968).

Petrides (1975) stressed a need to differentiate between principal foods and preferred foods in a diet. The former are items which are consumed in the greatest amounts, while the latter are items proportionally more abundant in the diet than available in the environment. Emlen (1966) stated that it is necessary to know factors other than the relative frequency of items in the diet and the abundance of food types in order to describe preferred foods.

The ecological availability of prey to the predator is related to a number of factors including: habitat and escape cover available to the prey; prey behavior, particularly as it relates to prey susceptibility; population densities of major prey and alternate prey; age, size, sex or experience of the predator; activity patterns of the prey and predator; climatic

influences such as snow accumulation; and social interactions within the predator population affecting the habitats accessible to an individual predator. Two other factors are important in the occurrence of prey in the diet; the fulfillment of the energy requirements of the predator, and the palatability of the prey to the predator.

Pine marten (*Martes americana*) often have been termed generalists to reflect the wide range of food items consumed and the tendency to omnivory during certain seasons. Despite the variety of foods consumed, Rosenzweig (1966) considers marten to be specialists with respect to the proportion of small prey in their diets. Some researchers believe marten to have a selection preference for certain small mammals (Cowan and Mackay 1950, Lensink et al. 1955, Weckwerth and Hawley 1962, Francis and Stephenson 1972, Douglass, R.J., L. Fisher and M. Mair, unpublished manuscript, Renewable Resources Consulting Services, Edmonton).

The objectives of the present study are:

a) to assess food selection within a population of pine marten located in the southern Northwest Territories, and relate food selection to the ecological availability of the principal prey species of the area;

b) to evaluate the success of the pine marten's predator strategy; and

c) to examine the effects of marten predation on the principal prey.

Because measurement of the ecological availability of prey involved many factors, data for the study were collected by various methods. Major emphasis was placed on radio-telemetry to provide information on marten activity and habitat use. Food habits were determined by analysis of marten scats and feeding trials with captive marten. Previous or concurrent studies at the Heart Lake Biological Station provided detailed information on small mammals, chiefly, red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) (Zirul 1970, Dyke 1971, Smith 1971, Stebbins 1971, Friesen 1972, Herman 1975, Fuller 1977, McPhee 1977).

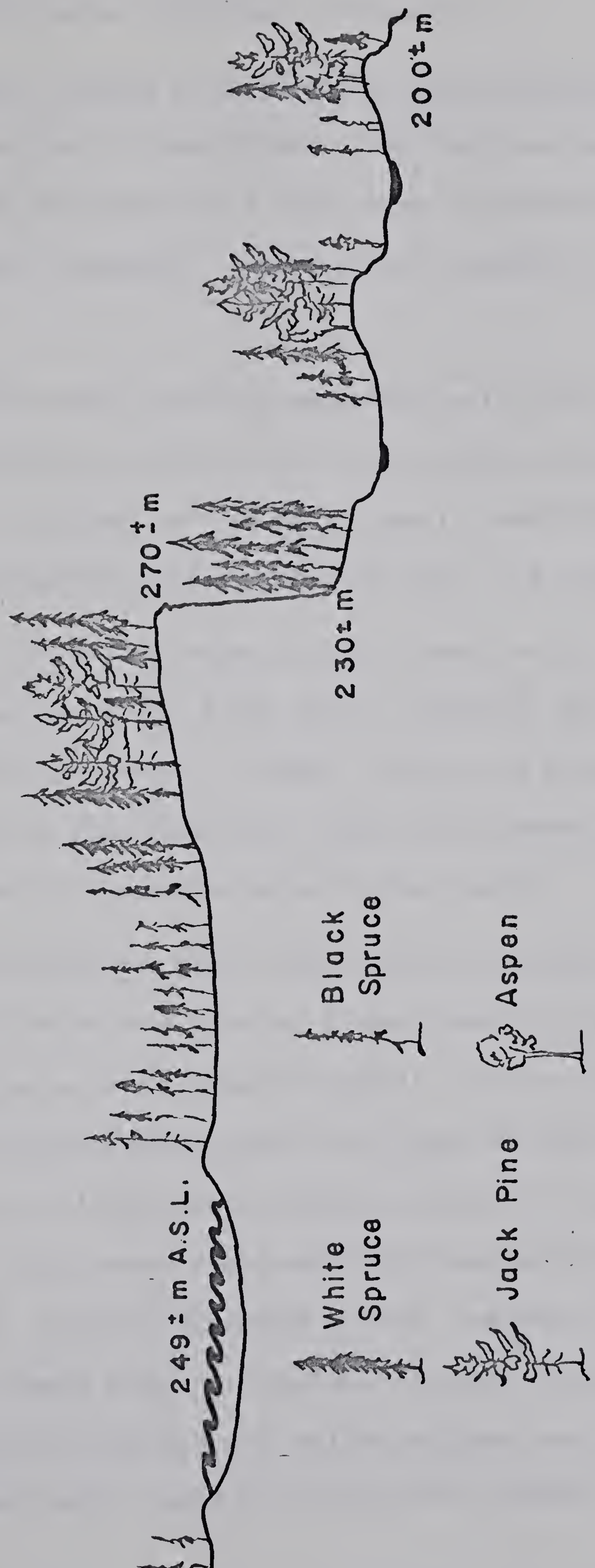
THE STUDY AREA

Field work was conducted from the Heart Lake Biological Station (60° 45' N, 116° 37' W) in the southern Northwest Territories. The study area was irregularly shaped, approximately 7.2 km by 3.2 km, between Kilometre Posts (KP) 124 and 133 on the Mackenzie Highway.

The landscape is generally flat to gently rolling. It is underlain by lower Paleozoic rocks - limestone, dolomite, shale, and minor deposits of sandstone - and is dominated by a sharp escarpment (Figure 1) up to 45 m above the former lake plain, where Upper Devonian limestone bedrock is exposed (Craig 1965). The local relief, otherwise, is a result of glacial and post-glacial deposits. There is a series of postglacial beach ridges between the escarpment and Great Slave Lake which appear as a series of sand and gravel terraces, roughly parallel to the escarpment (Craig 1965). Above the escarpment, soils are thin.

Four major soil series (Enterprise, Escarpment, Desmarais and Matou) occur in the study area (Day 1968). Enterprise soils are developed on moderately coarse or medium-textured beach deposits. They are Orthic Brown Wooded soils on gently sloping or level areas. The vegetation associated with this series is jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) with an understory of buffaloberry (*Shepherdia canadensis*), rose (*Rosa acicularis*), bearberry (*Arctostaphylos uva-ursi*), Labrador tea (*Ledum groenlandicum*), woody cinquefoil (*Potentilla fruticosa*), lichens (*Cladonia* spp.),

Figure 1. Profile of the Heart Lake study area (not to scale) and schematic presentation of the corresponding vegetation patterns.



249± m A.S.L.
270± m
230± m
200± m
White Spruce
Black Spruce
Jack Pine
Aspen

feather moss (*Hylocomium splendens*), and grasses.

The Escarpment complex is composed of similar beach materials with bare rock exposed in many places. The trees are usually well-spaced aspen and jack pine with a shrub layer of buffaloberry and juniper (*Juniperus communis*). Ground cover is bearberry, grasses, and lichens.

The Desmarais series are peaty materials over stony, gravelly loam. The vegetation is mainly black spruce (*Picea mariana*), tamarack (*Larix laricina*), willow (*Salix* spp.), dwarf birch (*Betula glandulosa*), cinquefoil, mosses (*Sphagnum* spp.), and sedges.

Matou soils are organic deposits over mineral soils. The vegetation is mainly willow, black spruce, tamarack, dwarf birch, Labrador tea, Sphagnum mosses, lichens, sedges, and grasses. There are extensive bogs with small lakes and a hummocky micro-topography, often with standing water in the troughs.

Well-drained abandoned beach ridge tops are dominated by jack pine and aspen with an understory of lichen, bearberry and bog cranberry (*Vaccinium vitis-idaea*) (Figure 2). South-facing slopes are dominated by white spruce with aspen and jack pine, while north-facing slopes usually support jack pine or aspen and white spruce. Black spruce dominated stands have understories of Labrador tea, crowberry (*Empetrum nigrum*), and moss. The troughs between beach ridges are variable in width; the vegetation is either ground birch muskeg with willow and some larch, or black spruce bogs with larch, ground birch and willow (Lindsey 1952).

Figure 2. Aerial photo mosaic of the Heart Lake study area.


Station
Heart Lake
126
128
130
0 Km
1
2
3
Kilometre Post

METHODS

Radio-Telemetry Equipment and Procedures

Marten were captured in 15 cm x 15 cm x 48 cm or 48 cm x 30 cm x 91 cm (first summer only) National live-traps using techniques described by Hawley (unpublished manuscript, Canadian Wildlife Service, Edmonton). During winter, the traps were insulated with sheets of styrofoam in order to keep the animals dry and as warm as possible. This technique was effective even when night temperatures dropped to -34°C.

Animals selected for radio collaring were anesthetized with sodium pentobarbital (More 1977). A radio transmitter (40 MHz range) with a brass collar, which also served as the transmitting antenna, was attached to the marten. After adjustment for size, the collar was soldered and wrapped in aluminum tape and electrician's tape to prevent neck abrasion. The frequency of the transmitter was then retuned. Animals were held until effects of the anesthetic wore off and then released at the point of capture. Both lithium chloride and mercury cells were used during portions of the study. Although the former resulted in lighter collars (20 - 22 g compared to 30 g), they did not last as long as expected and the use of lithium chloride cells was discontinued after the winter period. Theoretically, the maximum radio life should have been up to 200 days, but, in practice, was found to be up to 66 days.

Trails were established on an abandoned oil drilling access route below the escarpment and along its crest, along the Mackenzie Highway from KP 123 to 135, and along abandoned seismic lines south of the highway. Listening posts, marked by numbered tags, were established at about 200 m intervals. Topographic or vegetation features were used in the selection of listening posts to permit easy identification of the ground locations on aerial photographs. Signals were received from radio-tagged marten on a portable 12 volt receiver equipped with either a coil dipole antenna or a loop antenna. All equipment used in the study was built and supplied by the Bio-Electronics Unit of the Canadian Wildlife Service, Ottawa, with the exception of the loop antenna which was built by the Department of Electrical Engineering of the University of Alberta, Edmonton. Directional readings were taken with a Suunto compass attached to the antenna.

In the first summer and fall, the area was traversed on foot. In the winter, a Nordic snowmobile was used. During the second summer, a 55 cc Honda trailbike and a truck provided greater mobility. On four occasions, a Cessna 185 aircraft was used to locate animals that had dispersed out of range of the ground receiver. A dipole antenna was attached to the step of the aircraft, and flight lines, 400 m apart, were flown at an altitude of 150 m at an air speed of 140 kph. Upon detection of a signal, the area was criss-crossed until the strongest signal was obtained.

Times of tracking periods were set or modified by availability of transmitters and failure of receiving equipment. Sampling

times during a 24-hour period varied between seasons. Continuous 24-hour samples were attempted in all seasons except winter when low night-time temperatures caused the receiving equipment to freeze and malfunction. Tracking was carried out from August to October in 1974, and from January to March, and June to July in 1975.

Food Preference

Three marten, held in captivity at different times during the summer of 1974, were caged in three interconnected wire mesh cages (.6 m wide by 1 m deep by 1 m high). One cage contained a nest box of plywood with plexiglass ends to allow observation while enabling the animal to escape from insect harassment.

Because the first two captives, adult males, seemed to choose certain prey, a study was conducted to test the reaction of the third captive, a sub-adult female, when *C. gapperi* and *P. maniculatus* were offered simultaneously. Ten sessions included live prey (usually two of each species) while the remaining three included only dead prey.

Rate of Passage

'Labelled' mice were fed to the sub-adult female marten to determine the rate of passage. Two *C. gapperi* and two *P. maniculatus* were fed a mixture of uranine (sodium fluorescene),

peanut butter and lard into which finely cut wool threads had been mixed. Each mouse was given a mixture containing a different color of thread, so that the remains of each mouse could be positively recognized in the marten scats. The 'labelled' mice were presented simultaneously to the marten, which had been starved for 24 hours, and the time of consumption of each mouse was noted. All scats were collected at regular intervals, dried and passed under an ultra violet lamp. Those containing uranine were identified by the fluorescent glow and were examined for colored wool and teeth. In addition, the weight of all prey fed to this animal during the allotted period was recorded, and all scats were collected twice a day over the 23-day period that it remained in captivity.

Food Habits of Marten

Marten feces were collected throughout the study period as a regular part of all field work and during intensive searches at the end of each season. The age of scats found at the start of the study was estimated by the degree of decomposition. After the area had been cleared, the age of new scats could be estimated more accurately, particularly those deposited in winter months on snowmobile trails. Certain sites, including red squirrel (*Tamiasciurus hudsonicus*) middens and marten den sites, yielded high numbers of scats. Confusion of marten scats with those of other predators such as red fox (*Vulpes vulpes*) or fisher (*Martes pennanti*) was not a serious problem because of the low numbers of those species in the study area.

Four hundred and ninety-eight scats were judged to have been deposited between May, 1973 and August, 1975. Other scats which appeared to pre-date this period were discarded. In addition, three marten kill sites were found and included in the food habits observations. The scats were dried, broken apart and prey remains were examined under a dissecting microscope. Birds were identified to order, based on characteristics of the downy feather barbules (Day 1966). Mammals were identified to genus by hair characteristics (Adorjan and Kolenosky 1969), and to species by teeth and claws. Unidentified cricetid remains were apportioned between the species based on the frequency of occurrence of each species. A photo-key of teeth of small mammals known to occur in the study areas was made as a guide to identification. In addition, *C. gapperi* teeth were aged (Tupikova et al. 1968), and grouped in three age classes:

(i) groove closed - $<$ 2 months old;

(ii) roots formed - 2 - 8 months old;

(iii) roots $>$1 mm - $>$8 months old.

The second upper molar (M^2), on which this technique is based, was often not recovered. In these cases, another molar was substituted so that age assignments of prey were only approximate.

Seasons, to which scats were assigned, were chosen to relect changes in the physical environment. Spring was considered to be April and May when snow was melting and small mammal activity was increasing. June through August, characterized by long daylight hours and increasing small mammal numbers, were

considered summer. September and October, the period of highest small mammal numbers, increasing cold and shorter days, were assigned to fall. Winter comprised the longest time period, November to March, with snow cover, short cold days and, theoretically, decreasing availability of small mammals.

Small Mammal Indices

Small mammal trapping was carried out in 1974 and 1975 to gain information on faunal components of various habitat types, and the relative abundance of each species in those habitats. In May and July of 1974, 1,755 trap-nights (TN) were recorded on lines of 50 snap traps spaced 15 m apart in a variety of habitats. Vegetation was recorded at each trap site.

In early July of 1975, only five contiguous habitats - white spruce, aspen, black spruce -lichen, jack pine, and wet meadow - were each trapped for three nights with 100 snap-traps set at 15 m intervals. Data for 192 trap-nights in jack pine - juniper were furnished by S. Mihok (pers. comm.), and for 450 trap-nights in black spruce - lichen by D. Doyle (pers. comm.). A black spruce - sphagnum habitat was not sampled because of the limited success in this habitat in 1974.

Habitat Mapping

The vegetation of the study area was mapped by delineating major canopy types on aerial photographs (1:10,575), with the aid of a mirror stereoscope. Criteria for the mapping included fall color tones, vegetation texture, association of species, placement of habitats in relation to topography, and personal familiarity with various parts of the study area.

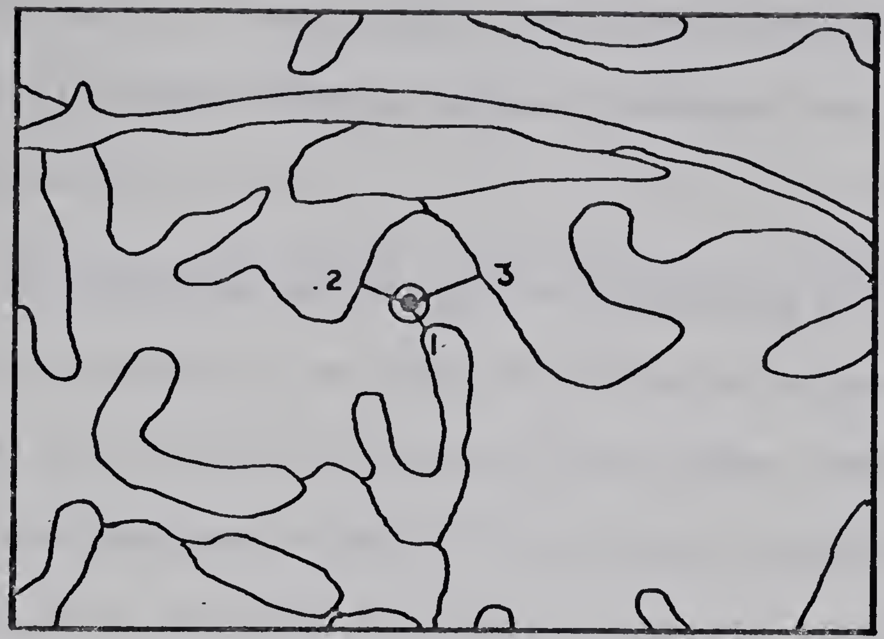
Seven major habitats were recognizable based on the dominant tree associations: black spruce - sphagnum, black spruce - lichen, white spruce - black spruce, white spruce - aspen, white spruce - jack pine, aspen, and jack pine - juniper habitats. Two further classes were standing water and exposed rock. Meadow habitats on the study area were too small to be identified by this method. Major habitats were further subdivided into five sub-classes according to the estimated percent canopy closure based on increments of 20 percent, from 0 to 100 percent.

Habitat Data Set

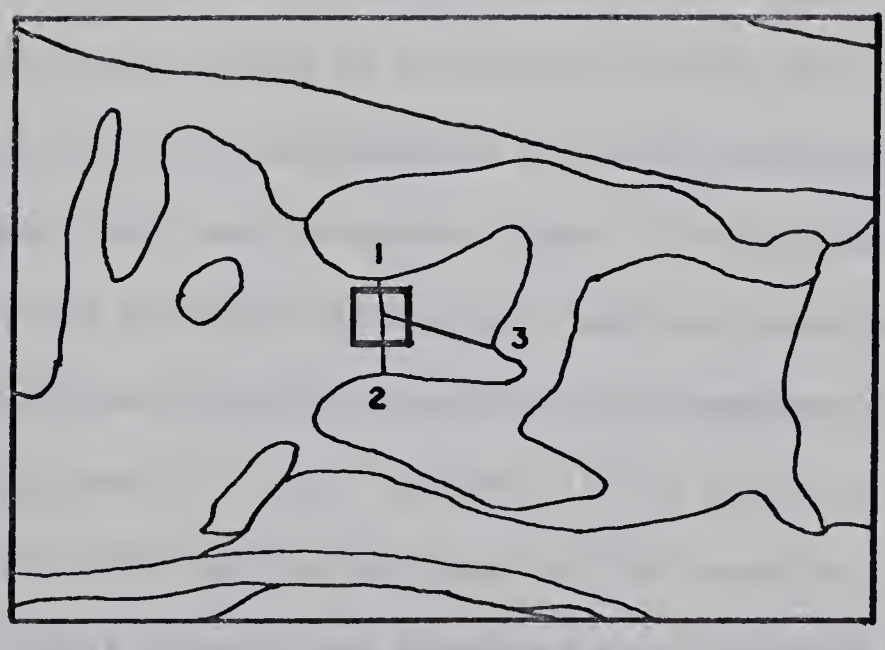
Three hundred and nineteen radio location points and trap site locations of marten were plotted on the habitat map. The habitat, canopy density, and the three closest habitats were recorded for each location (Figure 3).

A grid, with squares equivalent to ground distances of 77.7 m by 77.7 m, was constructed. This size was comparable to the size

Figure 3. Examples of the habitat data set for: a) marten radio locations and b) random samples. See text for explanation.



(a) Marten Location



(b) Random Location

of areas used by marten during short time periods (More, unpublished data). A random sample of 200 squares (10 percent of the study area) was made. The centre of each square was used to designate the habitat type. The three closest adjacent habitats were also recorded (Figure 3).

In order to determine whether marten used areas with high interspersion of habitats, an index of habitat heterogeneity was calculated for the marten locations and the random sample. A value of one was assigned to each of the closest habitats for every 100 feet that separated the habitat from the location or square centre. Values were summed for the three distances and an index number (from 1 to 5) was assigned by coding sums of 3-6 as 1, 7-9 as 2, 10-12 as 3, 13-15 as 4, and 16-18 as 5. The value one represented a location in a highly heterogeneous area while a value of five was considered as highly homogeneous.

An index of the degree of habitat mixture was useful for two reasons. First, no estimate of the error of each radio location was possible; therefore, the habitats for each location are not precise although they were treated as such. Second, delineation of habitats by use of aerial photographs was not absolute. These shortcomings were not considered serious in homogeneous habitats. In highly heterogeneous areas, however, it was possible that a marten was not in the habitat assigned to the location. This problem was minimal because few locations were recorded in highly heterogeneous habitats.

Activity Data

As the orientation of a radio collar changed, its radio signal strength varied. Steady signals meant that the marten was stationary; whereas fluctuating signals were attributed to movement. During each radio fix, the animal was recorded as either active or inactive.

Small Mammal Abundance by Habitat

An index of abundance of small mammals in each habitat was assigned based on the proportion of snap-traps catching small mammals. Values were arranged on a scale of five, ranging from absent (0) to abundant (4).

Similarly, a separate index of abundance in each habitat was calculated for *C. gapperi*, *P. maniculatus*, and meadow voles (*Microtus pennsylvanicus*). The abundance of each species in each habitat is considered to reflect the habitat preference of that species. The results of Dyke (1971), and Iverson and Turner (1973) were used to rate each sub-class of canopy density. Again, five values ranging from absent (0) to abundant (4) were used.

Other Ecological Parameters

Certain parameters tested in the model of habitat use and marten activity were collected in conjunction with the study.

Both time of day and weather were recorded when a marten was located. Maximum and minimum temperatures and barometric pressure were recorded at the Heart Lake Biological Station (W. A. Fuller, unpublished data). Times of sunrise and sunset, and phases of the moon were extracted from the Canadian Almanac and Directory (1974, 1975), and incoming daily solar radiation from Buffo et al. (1972).

Computer Program

The multivariate statistical method, Multiple Classification Analysis (MCA), used in this study to analyze habitat use and marten activity, was from the OSIRIS statistical package (University of Michigan 1973). MCA is essentially a multiple regression technique using dummy variables. It is able to handle predictors based on nominal measurements and interrelationships of any form among the predictors or between the dependent variable and a predictor. The model is additive so that the total variance is partitioned. The relationship between the dependent variable and an independent variable need not be linear as in a standard multiple regression procedure (Andrews et al. 1973). Runs of a single predictor variable result in a one-way analysis of variance. In this study, where the dependent variable is 0 or 1, the analysis is roughly equivalent to a two group discriminant function analysis.

MCA is designed to be theoretically or conceptually oriented, and indicates the magnitude of relationships between the dependent

and independent variables. Therefore, the end result is an aid to interpreting and describing the interrelationships. It usually is not applied to test statistical significance of a prediction.

Several statistics are calculated by the MCA program. The generalized squared multiple regression coefficient (Generalized R^2) measures the strength of the association of the dependent and independent variables. The bivariate statistics include the generalized eta-squared values (Eta^2) which represent the amount of variance of the dependent variable explained by each individual predictor. The eta values are a measure of the ability of the predictor to explain variation in the dependent variable. The beta values are a measurement of the ability of the predictor to explain this variation while holding constant all other predictors. The final statistic is the adjusted coefficient. This is an estimate of the effect of each level or sub-class for each predictor alone, after holding constant all other predictors.

RESULTS

Food Preference

A captive adult male marten, offered *C. gapperi* and *P. maniculatus*, left the *P. maniculatus*, but readily ate the *C. gapperi*.

A second adult male was given one dead *C. gapperi* and four live *P. maniculatus* on the morning of its capture. Twelve hours later, when two dead *C. gapperi* and three dead *P. maniculatus* were placed in the cage, all of the live mice were still active. By the following morning, the marten had escaped leaving six dead *P. maniculatus*. All *C. gapperi* and, presumably, the last *P. maniculatus* had been consumed.

Thirteen tests with a sub-adult female were conducted with only *C. gapperi* and *P. maniculatus* offered as food items. The results were ranked and tested by a Mann-Whitney U-test as all of the food tests includes more than one individual of each species. No preference was shown for one species or the other ($p > 0.05$). However, no definite conclusions are possible based on a sample of one animal. As the lack of preference of this marten conflicts with the evidence of the males, it may indicate that some individuals are less selective than others.

Rate of Passage

The female marten normally killed and consumed, within a short period of time, the four 'labelled' mice placed in the cage. In

the three tests conducted, the first remains of the mice were deposited 6.25, 8 and 6 hours after ingestion. The last marked remains were deposited 15, 14 and 19 hours after the last mice were consumed. In addition, a chipmunk (*Eutamias minimus*) fed to the marten, was partially deposited 10.5 hours after it was eaten. The mean number of scats (± SE) over a 23-day period was 8.2 ± 3.0 scats per day (range 4 - 15).

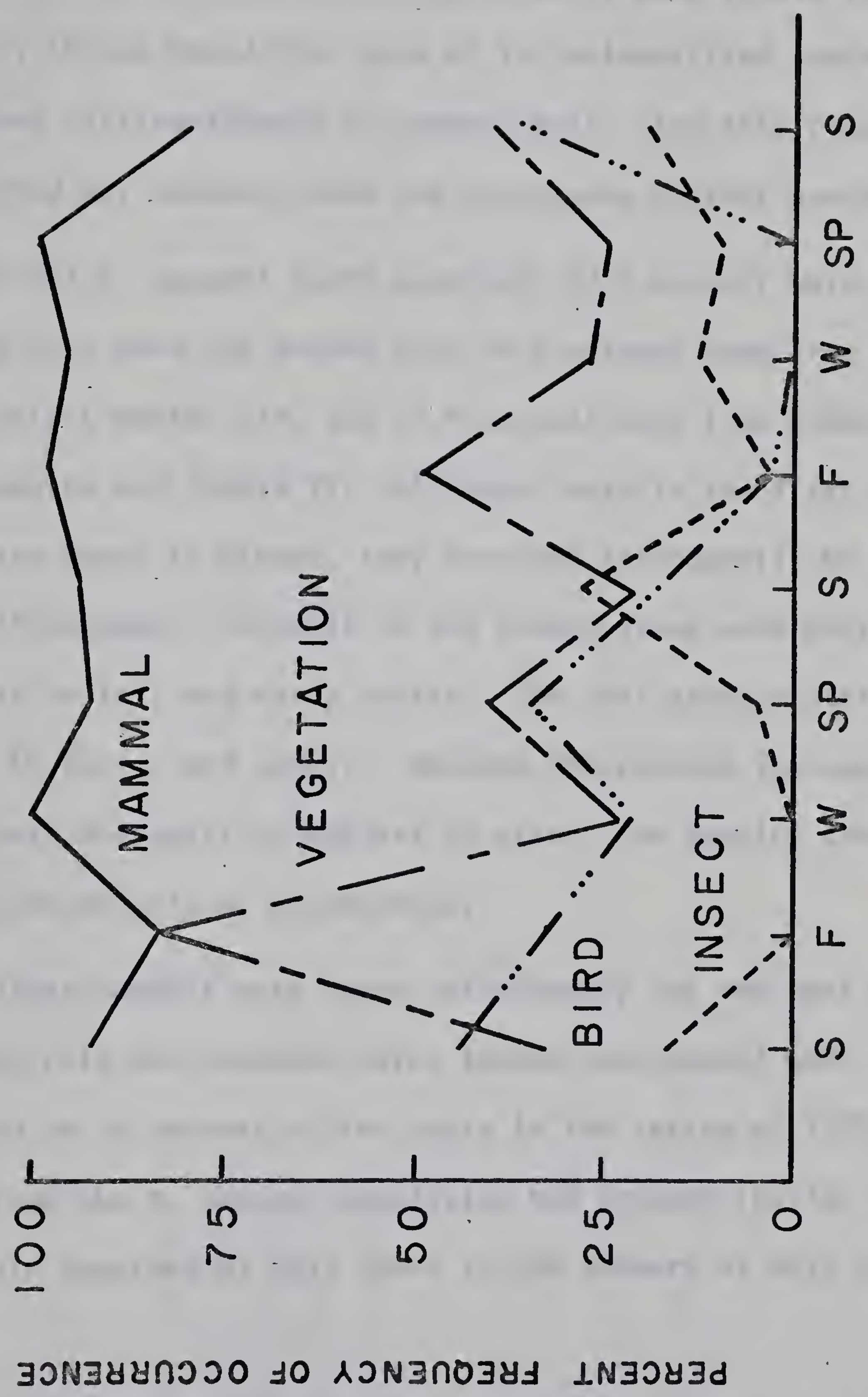
Food Habits of Marten

Occurrence of Prey Items

Mammals were the major food (95.2 percent) of marten throughout the study period (Figure 4, Appendix 1). The most commonly occurring species were *C. gapperi* and *M. pennsylvanicus*. Two species, *P. maniculatus* and *E. minimus*, which were prevalent in some habitats, were conspicuously low or absent in scat contents. In addition, several rare mammal species - jumping mouse (*Zapus hudsonicus*), woodchuck (*Marmota monax*), and little brown bat (*Myotis lucifugus*) - were not found in scats.

The importance of mammals in the diet of marten was evident by the high occurrence of mammal items (1.2 per scat) in marten scats (499). This average increased to 1.3 items per scat when only scats with mammal remains (475) are considered. Cricetid remains occurred most frequently (1.1 per scat) in the latter sample.

Figure 4. Percent frequency of occurrence of major components of marten food by season, 1973-75.


PERCENT FREQUENCY OF OCCURRENCE
100
75
50
25
0
MAMMAL
VEGETATION
BIRD
INSECT
S
F
W
SP
S
F
W
SP
S
1973
1974
1975

As the small mammals were identified only by teeth, it was necessary to apportion scats with unidentified cricetid remains among the known species according to their occurrence, in an attempt to compare the importance of each (Table 1). However, it was noted that many of the unidentified scats contained distinguishable *C. gapperi* hair. For this reason, the method may underestimate the occurrence of that species.

Of 263 *C. gapperi* teeth examined, 37.2 percent were from animals less than two months old, 44.8 percent were from those two to eight months old, and 17.9 percent were from those over eight months old (Table 2). Although teeth in the first category were found in winter, they occurred infrequently by the month of November. Animals in the second group were most frequent in fall and early winter. The last group occurred mainly in spring and summer. Because determining the age of both teeth and scats is subject to error, the results should be considered only as an estimate.

Larger mammals were taken infrequently for the most part. Red squirrels and snowshoe hares (*Lepus americanus*) each occurred in 10 percent of the scats in the spring of 1975, by which time the *C. gapperi* population had crashed (Fuller 1977). Squirrels remained at this level in the summers of both 1974 and 1975.

Shrews (*Sorex cinereus* and *Microsorex hoyi*) varied considerably between seasons. *S. cinereus* occurred less often in 1974 when small rodent numbers peaked, than in 1973 or 1975.

Table 1. Adjusted* percent occurrence of cricetid species in marten scats, 1973-75.

SPECIES	1973		1974				1975			1973-75
	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Total
Clethrionomys gapperi	52	83	53	43	67	91	45	80	40	71
Microtus pennsylvanicus	48	-	32	28	29	20	36	20	24	24
Phenacomys intermedius	-	-	4	-	2	-	4	-	4	2
Synaptomys borealis	-	-	4	12	4	4	4	-	12	5
Peromyscus maniculatus	-	-	4	22	8	2	4	-	12	7
Number of scats	25	6	47	51	131	86	110	20	25	501

* Unidentified cricetid remains apportioned between species.

Table 2. Age-classes of *Clethrionomys gapperi* teeth in marten scats by season, 1973-75.

SEASON	YEAR	AGE CLASS: <2 months old (anterior groove closed)		2-8 months old (roots formed)		>8 months old (roots >1 mm)		TOTAL
		No.	Percent	No.	Percent	No.	Percent	
Summer	1973	4	36	4	36	3	27	11
Fall	1973	1	25	2	50	1	25	4
Winter	1973-74	7	50	4	29	3	21	14
Spring	1974	0	--	6	60	4	40	10
Summer	1974	25	38	21	32	19	29	65
Fall	1974	36	58	19	31	7	11	62
Winter	1974-75	21	27	49	64	7	9	77
Spring	1975	0	--	5	36	9	64	14
Summer	1975	4	67	1	17	1	17	6
		98	37	118	45	47	18	263

M. hoyi were present in significant numbers only during the winter of 1974-75 as rodent populations declined (Appendix 1).

In overall occurrence, birds ranked third (18.8 percent) (Figure 4). No seasonal trends are apparent, but birds of the Orders Galliformes (mostly spruce grouse *(Canachites canadensis)*) and Passeriformes occurred in all seasons in the scats (Appendix 1). A variety of passerine and non-passerine species occur in the summer (Carbyn 1971), but few are winter residents. The most common breeding birds are from the Fringillidae and Parulidae.

Although vegetation ranked second in importance based on the frequency of occurrence (32.3 percent) (Figure 4), many scats contained only trace amounts. Fall was the period of greatest consumption of fruits. During that season, several scats consisted primarily, or solely, of seeds and berry coats (Appendix 1). While it is possible that the traces of grass and needles were accidentally ingested with prey, berries were deliberately sought.

Fruits of only four plant species were of notable quantity and frequency of occurrence: common bearberry, crowberry, raspberry (*Rubus strigosus*), and rose. All species, except crowberry, have fruits which overwinter and retain some berries until new ones ripen the following year (Dyke 1971). The fruits of the first three species ripen mid to late July, while those of the roses ripen half a month later. Variation in annual berry production was reflected in the occurrence of that species in the scats.

Invertebrate remains were scarce (11.4 percent) and were limited to summer periods (Figure 4, Appendix 1). These were mainly bald-faced hornets (*Vestula maculata*) while a few were bees of an undetermined species. A few scats were composed entirely of these insects, often with a waxy substance. The latter is presumably the combs from the nests.

Relative Biomass

The relative biomass of mammal species was estimated by multiplying the mean weight of each species by its frequency of occurrence in the marten scats (Table 3). This method assumes that each occurrence represents only one individual prey. In cases of large prey, a bias is introduced because a single prey item would undoubtedly have been deposited in a large number of scats. Estimates for *L. americanus* and grouse, therefore, may be unreliable as an indication of the importance of these species in the diet of marten and are ommitted.

For small mammals, the relative biomass estimate shows that *M. pennsylvanicus* were almost one half as important as *C. gapperi*, and *P. maniculatus* were only one tenth as important as *C. gapperi*. In 1974, the relative biomass of *C. gapperi* was very high during the peak in vole numbers.

Shrews accounted for only a small proportion of the overall relative biomass and showed a wide seasonal fluctuation in occurrence. It was difficult, if not impossible, to determine the accuracy of the relative biomass estimate for *T. hudsonicus*.

Table 3. Relative biomass (g) of mammals represented in marten scats from 1973-75*. Average adult weights after Soper (1964).

SPECIES	1973 Summer	1973 Fall	1974 Winter	1974 Spring	1974 Summer	1974 Fall	1975 Winter	1975 Spring	1975 Summer	1973-75 Total
Clethrionomys gapperi	339	130	652	574	2 297	2 036	2 584	418	261	9 291
Microtus pennsylvanicus	382	--	477	445	1 208	541	445	159	191	3 848
Phenacomys intermedius	--	--	59	--	88	--	59	--	29	235
Synaptomys borealis	--	--	50	150	125	75	125	--	75	600
Peromyscus maniculatus	--	--	49	269	269	49	98	--	73	807
Tamiasciurus hudsonicus	238	--	476	238	2 855	714	1 903	476	714	7 614
Glaucomys sabrinus	--	--	158	--	--	--	--	--	--	158
Sorex cinereus	7	--	7	4	4	4	4	4	4	38
Sorex arcticus	9	--	--	--	--	--	26	--	--	35
Microsorex hoyi	--	--	--	--	6	3	26	--	--	35
Number of scats	25	6	47	52	131	86	110	20	25	501

* Unidentified remains proportioned between known species.

Although it was obviously important as a prey item when caught, the total relative biomass is probably highly overstated by this technique.

Calculation of Total Small Mammals Consumed

The number of days spent by each marten on the study area was estimated from the percent of days on which the animal was located during the radio-tracking periods (Table 4). For animals not radio-collared, an estimate was made based on live-trap data (Table 4). The number of marten days was multiplied by an average defecation rate of 8.2 scats per day to estimate the total number of marten scats deposited on the study area each season (Table 5). Then, the total number of all cricetids consumed by marten each season was estimated (Table 5). The number of each species consumed for each season was calculated using the proportion of each small mammal species from food habits in the Heart Lake study area (Table 6, Appendix 1). A crude approximation of the total biomass of each species consumed by marten was obtained by multiplying the total of each species by the mean weight of that species (Table 6). The total biomass estimate was reduced by four percent (15 428 g) (Lockie 1959, 1961, Goszczynski 1974) to derive an estimate of the total digestible biomass (370 268 g) of small mammals consumed.

The importance of *C. gapperi* compared to other small mammals is readily apparent (Table 6). Numerically, *M. pennsylvanicus* were one third as important as *C. gapperi* and

Table 4. Estimated days spent on the study area by each marten from 1973-75.

Animal	Sex[a]	Age[b]	Dates Present	% Time on Study Area	Estimated Number of Days on Study Area
R1	F	Ad	June 1/73 - August 15/75	10	80
R2	F	Sa	June 1/73 - August 30/74*	20	87
R3	M	Ad	June 1/73 - May 31/75	36	262
R4	M	Ad	June 1/73 - March 12/75	33	214
R5	F	Jv	June 1/74 - August 15/75	30	132
R6	F	Jv	June 1/74 - May 31/75	8	32
R7	F	Jv	June 1/74 - August 22/74	50[c]	42
R8	M	Ad	June 1/73 - August 15/75	30	242
R9	M	Jv	June 1/74 - August 30/74	50[c]	46
R0	F	Jv	June 1/74 - August 30/74	50[c]	46
W1	M	Ad	June 1/73 - May 31/75	5	37
W2	F	Ad	? - January /75	?	8
W3	M	Ad	June 1/73 - August 15/75	20	158
W4	M	Jv	June 1/75 - August 15/75	50[c]	38
W5	M	Jv	June 1/75 - July 18/75	50[c]	24
W6	M	Sa	? - August 1-15/75	50[c]	15
					1,463

a M = Male F = Female

b Age when first captured: Ad = Adult, Sa = Sub-adult, Jv = Juvenile

c Young of year - estimated percent time only; assumes limited movement.

* Excluding June 30 - July 22, 1974 when held in captivity.

Table 5. Estimated total number of Cricetidae consumed by marten on the Heart Lake study area from 1973-75.

Season	Year	Estimated[a] Scat Total	% Scats with Cricetidae	Total Scats with Cricetidae	Number of Cricetidae per Scat	Total[b] Cricetidae	Number Per 30 Days
Summer	1973	1 153	88	1 015	1.14	1 157	386
Fall	1973	765	100	765	1.00	765	382
Winter	1973/74	2 658	85	2 259	1.15	2 598	519
Spring	1974	765	84	643	1.23	791	395
Summer	1974	2 433	89	2 165	1.24	2 685	895
Fall	1974	854	98	837	1.19	996	498
Winter	1974/75	2 982	88	2 624	1.28	3 359	671
Spring	1975	594	95	564	1.11	626	313
Summer	1975	1 191	72	858	1.28	1 098	366

a Marten days (Table 4) multiplied by average defecation rate.

b Modified from Ryszkowski et al. 1971.

Table 6. Estimated number and total biomass of cricetid species consumed each season by marten on the Heart Lake study area from 1973-75.

SPECIES	1973 Summer	1973 Fall	1973 Winter	1974 Spring	1974 Summer	1974 Fall	1974 Winter	1975 Spring	1975 Summer	Total Numbers	Total Biomass (g)
C. gapperi	602	765	1 412	328	1 630	777	2 682	477	477	9 150	238 815
M. pennsylvanicus	555	--	847	209	704	169	379	166	286	3 315	105 417
P. intermedius	--	--	113	--	56	--	54	--	48	217	7 940
S. borealis	--	--	113	90	93	30	135	--	143	604	15 100
P. maniculatus	--	--	113	164	204	20	108	--	143	752	18 424
										14 038	385 696

almost one half as important in terms of the biomass contributed to the diet of marten. This species was especially important in years which were not peak years for *C. gapperi*.

Although *P. maniculatus* were almost as abundant in snap-trap samples as *C. gapperi* in white spruce upland habitats (W. A. Fuller, pers. comm.), they were not consumed by marten in similar proportions (Table 6).

Food Requirements of Marten

Farrell and Wood (1968) reported that the digestible daily food requirement for maintenance (heat production, thermal regulation, activity, and fur growth) of adult female mink (*Mustela vison*) was: Intake (g) = 0.226 weight (g) + 14. Because temperatures were above 7°C (daily mean, 10.7°C) and activity was reduced in the small cages used, the formula would underestimate the requirement of free-ranging marten, assuming that the physiological systems of the two species are similar. However, the formula was used to calculate the minimum digestible daily food intake and the total digestible food intake for each marten during the time spent on the study area (Table 7). The average required intake of digestible biomass by marten was 274 g per day (range 158 - 364 g per day). Large adult male marten required up to 364 g per day ($\bar{X}$ = 315 ± 33 g per day), while juveniles required as little as 158 g per day ($\bar{X}$ ♂ + ♀ = 213 ± 55 g per day). Adult and sub-adult females required 206 ± 9 g per day. The minimum total of digestible biomass

Table 7. Calculated* daily and total digestible food intake requirement of marten on the study area from 1973-75.

Marten	Calculated Daily Digestible Food Intake (g)	Calculated Total Digestible Food Intake (g)
R1	217	17 501
R2	206	17 843
R3	285	74 722
R4	285	61 076
R5	209	27 575
R6	195	6 234
R7	195	8 182
R8	364	88 161
R9	206	9 481
R0	172	7 921
W1	310	11 459
W2	195	1 559
W3	330	52 203
W4	234	8 905
W5	158	3 780
W6	297	4 448
		401 050

* After Farrell and Wood (1968)

Intake (g) = 0.226 weight (g) + 14.

consumed by marten on the study area from 1973-75 was estimated to be 401 050 g or 0.25 g/ha/day.

An opportunity to check the calculated minimum digestible daily food intake was provided by the captive female marten. This individual was fed 4 000 g of small mammals and birds during a 23-day period of captivity. Assuming that four percent of this biomass was undigestible matter (Lockie 1959), the daily intake of digestible matter was 174 g per day. The weight of the marten was 850 g when captured and 950 g when released. Marten daily food requirements may be less than those of mink since the female marten gained 100 g during a 23-day period of reduced activity in a warm month while on a lower food intake than its calculated requirement of 206 g per day.

Small Mammal Numbers and Habitat Preferences

The habitat preferences of *C. gapperi*, *P. maniculatus*, and *M. pennsylvanicus* were based on the number of each species caught per 1,000 trap-nights in each habitat (Table 8). *C. gapperi* occurred in greatest numbers in aspen and white spruce habitats, followed by jack pine, jack pine - juniper, and black spruce - lichen. *P. maniculatus* were most common in jack pine - juniper, followed by aspen and jack pine. *M. pennsylvanicus* were abundant in meadow habitats and absent in all other habitats except black spruce - lichen. The only specimen caught in black spruce - sphagnum was a single *M. hoyi*.

Table 8. Habitat preference of three small mammal species in the Heart Lake study area in the summers of 1974 and 1975.

HABITAT TYPE	SPECIES OF SMALL MAMMAL *Clethrionomys gapperi* No. per 1000 trap nights	*Peromyscus maniculatus* No. per 1000 trap nights	*Microtus pennsylvanicus* No. per 1000 trap nights	Total per 1000 trap nights
Aspen	50	17	0	67
Meadow	16	3	47	66
Jack Pine - Juniper	31	26	0	57
White Spruce	49	6	0	55
Jack Pine	32	16	0	48
Black Spruce - Lichen	31	0	7	38
Black Spruce - Sphagnum	0	0	0	0

A total small mammal catch was calculated for each habitat (Table 8). Aspen and meadow habitats were the most productive, while black spruce - sphagnum was the least productive habitat. This estimate of the production for each habitat must be considered only a rough approximation due to the sampling technique and the small sample sizes.

Habitat Use

Seasonal use of habitat by marten was analyzed by comparing a random sample of habitats available on the study area with the habitats in which marten were located during telemetry surveys. Because the spring sample size was low, it was grouped with summer data.

In order to determine if there was a difference in the two sets of data (radio locations and random sample) before undertaking an examination of the habitat use model, a one-way analysis of variance was performed. A statistically significant difference in relative habitat use indicated that marten did not use the habitat in a random manner. This difference was higher for the fall and winter seasons ($p < 0.01$) than for summer ($p < 0.05$).

In a similar fashion, the same test was performed to decide if there was a difference in the heterogeneity of the vegetation in the two sets of data. No statistically significant difference ($p > 0.05$) was found.

A normal MCA analysis was performed for each of the three seasons by comparing marten location points with the random sample. The strength of the relationship (Generalized R^2) between habitats used by marten against a random sample of habitats and independent (predictor) variables of habitat at the location and closest three habitats was calculated. The habitat predictors explained 42, 58 and 51 percent of the variance between the two data sets in summer, fall and winter, respectively (Table 9). As the interspersion of habitats is important for a variety of reasons (including availability of cover, den sites, and prey), the analysis is a test of the importance of the habitat at the points where marten were located and the surrounding habitats.

Generalized eta^2 values indicated the usefulness of the habitat predictors. Each accounted for 11 to 15 percent of the variance in summer, 20 to 27 percent in fall and 18 to 22 percent in winter (Table 9). Beta values revealed that, in general, the habitats at the radio location and the two closest habitats were the best predictors. The third closest habitat was the weakest predictor (Table 9). The discrepancy among the predictors as to the best predictor is explained by the closeness of the habitats to the radio location habitat. Of the 319 first closest habitats, 255 were less than 61 m from the radio locations. Similarly, 129 of the second nearest habitats were closer than 61 m. Only 49 of the third closest habitats were closer than 61 m. As the distance from the radio location increased, the predictor ability of each habitat predictor decreased.

Table 9. Summary statistics of marten habitat predictors.

Predictor	Statistic	Summer	Fall	Winter
Radio location habitat	Beta	0.413	0.443	0.401
	Eta	0.337	0.511	0.434
	Eta^2	0.114	0.261	0.188
1st closest habitat	Beta	0.492	0.364	0.392
	Eta	0.332	0.447	0.433
	Eta^2	0.146	0.200	0.188
2nd closest habitat	Beta	0.362	0.436	0.383
	Eta	0.380	0.518	0.472
	Eta^2	0.144	0.269	0.223
3rd closest habitat	Beta	0.273	0.288	0.353
	Eta	0.354	0.481	0.418
	Eta^2	0.125	0.232	0.175
	Generalized R^2	0.423	0.582	0.508

Where a comparison is being made between a non-random sample of marten locations and a random sample of possible habitats, a positive value indicates greater than expected use and a negative coefficient indicates less than expected use of habitats on the study area by marten. Appendix 2 presents the coefficients for each sub-class of habitat for the independent variables offering good predictor ability. Sub-classes which did not contain data cases were omitted in the computer runs.

As the number of cases may radically change the magnitude of the coefficients, the results were grouped into categories of 1-5, 6-15, 16-25, and greater than 25. The sample size of the first category rendered it unreliable and it was excluded from further interpretation. The coefficients were only used to conceptualize marten habitat use. They were not considered reliable as expressions of statistical probabilities.

Seasonal habitat use by marten is shown in Table 10. In summer, marten showed a greater than expected use of mesic habitats, mostly coniferous and deciduous stands of moderate to high stand density. Habitats which received less than expected use included open habitats of coniferous or mixed deciduous stands. Trends for fall and winter were similar, with the exception of closed aspen stands which were not used in winter. It would seem that closed mixed coniferous and mixed deciduous stand types, that is, typically mesic sites, were used most frequently. Open xeric or open moist sites were used least. Use of habitats in the range between the two extremes was not as clear cut, indicating

Table 10. Greater or less than expected use of habitat types by marten compared with a random sample of available habitats by season.

SAMPLE SIZE	SUMMER Greater than expected	SUMMER Less than expected	FALL Greater than expected	FALL Less than expected	WINTER Greater than expected	WINTER Less than expected
25	WS-JP e A e	JP-J b BL-L d	WS-JP e * A e		WS-JP e	JP-J b
16-25	WS-JP d	BS-S b WS-A e WS-JP c *		BS-S b WS-BS b * BS-L d JP-J b	WS-JP c *	BS-S b * BS-L d
6-15	WS-A d WS-BS c BS-L c	WS-BS b	WS-BS c WS-JP c *	WS-A e WS-JP d * BS-L c *	WS-A c WS-BS c BS-L c *	WS-A e * WS-BS b * WS-JP d A e

Canopy Density (Percent): b = 21-40, c = 41-60, d = 61-80, e = 81-100.

Abbreviations: WS = White Spruce, BS = Black Spruce, JP = Jack Pine, A = Aspen, L = Lichen, S = Sphagnum, J = Juniper.

* Coefficient value approaches zero indicating minimal difference between groups.

that these areas were used in varying degrees. The use of moderately open black spruce - lichen or white spruce stands may be explained by the presence of small meadows or grassy openings.

Although one would intuitively expect closely positioned habitats to show some degree of interdependence, this may be modified by topography, soil, drainage, or drastic local ecological changes such as fire. The first and second closest habitats to the marten locations showed a greater than expected occurrence of mixed coniferous and mixed deciduous stands of moderate to high stand density. Open habitats, particularly on dry or wet sites, occurred less frequently than expected in the summer, fall and winter (Tables 11, 12).

Small Mammal Prevalence

A major factor governing the use of a habitat by a predator is the prevalence of prey species. An index of abundance value for each species was assigned to each habitat in the data sets for the marten locations and the random sample. Analyses for each season were performed for the following: all small mammals, *C. gapperi*, *P. maniculatus*, and *M. pennsylvanicus*. Predictor variables included the prevalence of each species or all small mammals at the location points, and the prevalence of each species or all small mammals in each of the three closest habitats. The interspersion of habitats alters prey numbers and species composition.

Table 11. Greater or less than expected occurrence of habitat types closest to the marten location points compared with a random sample of habitats by season.

SAMPLE SIZE	SUMMER Greater than expected	SUMMER Less than expected	FALL Greater than expected	FALL Less than expected	WINTER Greater than expected	WINTER Less than expected
25	WS-JP e	BS-S b *	WS-JP c	BS-S b *	WS-JP e	BS-S b
		BS-L d	WS-JP e *		JP-J b *	
		JP-J b				
16-25	WS-A c		WS-A c	BS-L d	WS-A c	BS-L d
	WS-JP c *			WS-JP d *	WS-JP c	
				WS-JP d *		
6-15	BS-S c	JP-J a	WS-A d *	WS-BS d *	WS-A d	A e
	BS-L c *		WS-A e	JP-J a	WS-A e *	
	WS-A e		WS-BS b *		WS-JP b *	
	WS-JP b *		A e		WS-JP d	
	WS-JP d				WS-BS d	
	WS-BS d *					
	A e					

Canopy Density (Percent): a = 0-20, b = 21-40, c = 41-60, d = 61-80, e = 81-100.

Abbreviations: WS = White Spruce, BS = Black Spruce, JP = Jack Pine, A = Aspen, L = Lichen, S = Sphagnum, J = Juniper.

* Coefficient value approaches zero indicating minimal difference between groups.

Table 12. Greater or less than expected occurrence of habitat types second closest to the marten location points compared with a random sample of habitats by season.

SAMPLE SIZE	SUMMER		FALL		WINTER	
	Greater than expected	Less than expected	Greater than expected	Less than expected	Greater than expected	Less than expected
25	WS-JP d * WS-JP e *	BS-S b	WS-A d * WS-JP e *		WS-JP e	BS-S b *
16-25	BS-L d WS-A c JP-J b *	WS-A d	WS-A e WS-JP c WS-JP d *	BS-S b	WS-A c WS-JP c JP-J b *	WS-A d WS-JP d
6-15	WS-BS c WS-JP b WS-JP c JP-J a	BS-S a BS-L c * WS-A e * WS-BS d Water	BS-L d *	BS-S a BS-L c * WS-A c * WS-BS d * JP-J a JP-J b Water	BS-L d * WS-A e *	BS-S a * BS-L c WS-JP b JP-J a WS-BS d * A e * Water

Canopy Density (Percent): a = 0-20, b = 21-40, c = 41-60, d = 61-80, e = 81-100.

Abbreviations: WS = White Spruce, BS = Black Spruce, JP = Jack Pine, A = Aspen, L = Lichen, S = Sphagnum, J = Juniper.

* Coefficient value approaches zero indicating minimal difference between groups.

The generalized R^2 value for each analysis showed that no one prey species accounted for more than 23 percent of the variance of the dependent variable (Table 13). Of the four analyses, the prevalence of *C. gapperi* was most useful in terms of explaining marten use of habitats. The prevalence of *M. pennsylvanicus* was least useful. The limited ability of the model to explain variance may reflect the overlap of habitats preferred by *C. gapperi* and *P. maniculatus*, and the restricted number of habitats preferred by *M. pennsylvanicus*, and the interaction of values for habitats close to the radio location. In addition, the lack of a refined index of prevalence for each species may be important.

When the coefficients for each season for all four analyses are examined (Appendix 3), certain trends are readily apparent. There was greater than expected use of areas with moderate to high prevalence of all small mammals, and of *C. gapperi*. Conversely, little use was made of habitats with low prevalence of either group. Although *P. maniculatus* were not rated as high in prevalence because of the very high numbers of *C. gapperi* in 1974 (W. A. Fuller, unpublished data), there was greater than expected use of habitats with moderate prevalence of the former species. This is not unexpected since the overlap in habitat preference was substantial. There was little use by marten of habitats where *M. pennsylvanicus* were considered to be abundant. It is evident either that marten were very successful in capturing *M. pennsylvanicus*, or that the number of this species were underrated in certain habitats. Alternatively, the study may not have adequately measured marten use of habitats preferred by *M. pennsylvanicus*.

Table 13. Summary statistics of small mammal prevalence at the radio locations and the three closest habitats compared with a random sample.

Species	Statistic	Predictor*	Summer	Fall	Winter
All small mammals	Beta	1	0.259	0.336	0.157
		2	0.226	0.129	0.215
		3	0.178	0.263	0.232
		4	0.070	0.126	0.065
	Eta^2	1	0.219	0.302	0.172
		2	0.196	0.144	0.233
		3	0.187	0.257	0.289
		4	0.105	0.091	0.092
	Generalized R^2		0.138	0.197	0.143
C. gapperi	Beta	1	0.313	0.380	0.221
		2	0.284	0.199	0.205
		3	0.177	0.218	0.130
		4	0.084	0.153	0.137
	Eta^2	1	0.230	0.333	0.194
		2	0.198	0.201	0.192
		3	0.197	0.224	0.161
		4	0.076	0.122	0.130
	Generalized R^2		0.166	0.229	0.117
P. maniculatus	Beta	1	0.248	0.296	0.135
		2	0.286	0.212	0.257
		3	0.229	0.181	0.216
		4	0.121	0.114	0.086
	Eta^2	1	0.183	0.322	0.259
		2	0.242	0.270	0.335
		3	0.232	0.250	0.316
		4	0.019	0.253	0.189

Species	Statistic	Predictor*	Summer	Fall	Winter
P. maniculatus	Generalized R^2		0.162	0.201	0.189
M. pennsylvanicus	Beta	1	0.130	0.244	0.155
		2	0.266	0.192	0.236
		3	0.197	0.202	0.176
		4	0.232	0.034	0.047
	Eta^2	1	0.124	0.257	0.216
		2	0.197	0.259	0.307
		3	0.201	0.212	0.215
		4	0.127	0.158	0.132
	Generalized R^2		0.130	0.143	0.140

* 1 = location points, 2 = first closest habitat, 3 = second closest habitat, 4 = third closest habitat.

Marten Activity

Activity patterns of a predator are affected by factors such as inclement weather, extreme temperatures and previous hunting success. Each time a radio-tagged marten was located, it was recorded as active (1) or inactive (0). The interrelationships of this dependent variable and several independent variables including weather (clear, overcast, rain, or snow), moon phase, time of day, time of sunrise and sunset, daily maximum and minimum temperatures, barometric pressure, direct incoming solar radiation, habitat type, and proximity to the escarpment were analysed using MCA. Of these predictor variables only weather, time of day, and habitat type were retained in the final analysis; the other predictors were deleted because of the limited contribution to the explanation of variance. It is possible that some of the deleted predictors could have been of value if either more precise measurements had been taken at the time of the radio fixes, or greater extremes for certain variables had occurred during the tracking periods.

The three predictors provided limited explanation of the activity analysis (Table 14). Although they explained 33 percent of the variance in summer, they explained only 16 and 20 percent of the fall and winter variance, respectively. The individual explanation contributed by each predictor was low and varied among seasons. The eta^2 values ranged from 2 to 24 percent in summer, 5 to 6 percent in fall, and 1 to 11 percent in winter. Time of day was the best predictor in summer and winter; while weather

Table 14. Summary statistics of marten activity predictors.

Predictor	Statistic	Summer	Fall	Winter
Time	Beta	0.526	0.273	0.426
	Eta	0.487	0.254	0.325
	Eta^2	0.237	0.065	0.106
Weather	Beta	0.161	0.285	0.283
	Eta	0.145	0.241	0.218
	Eta^2	0.021	0.058	0.048
Habitat	Beta	0.289	0.224	0.196
	Eta	0.289	0.217	0.110
	Eta^2	0.083	0.047	0.012
	Generalized R^2	0.331	0.164	0.202

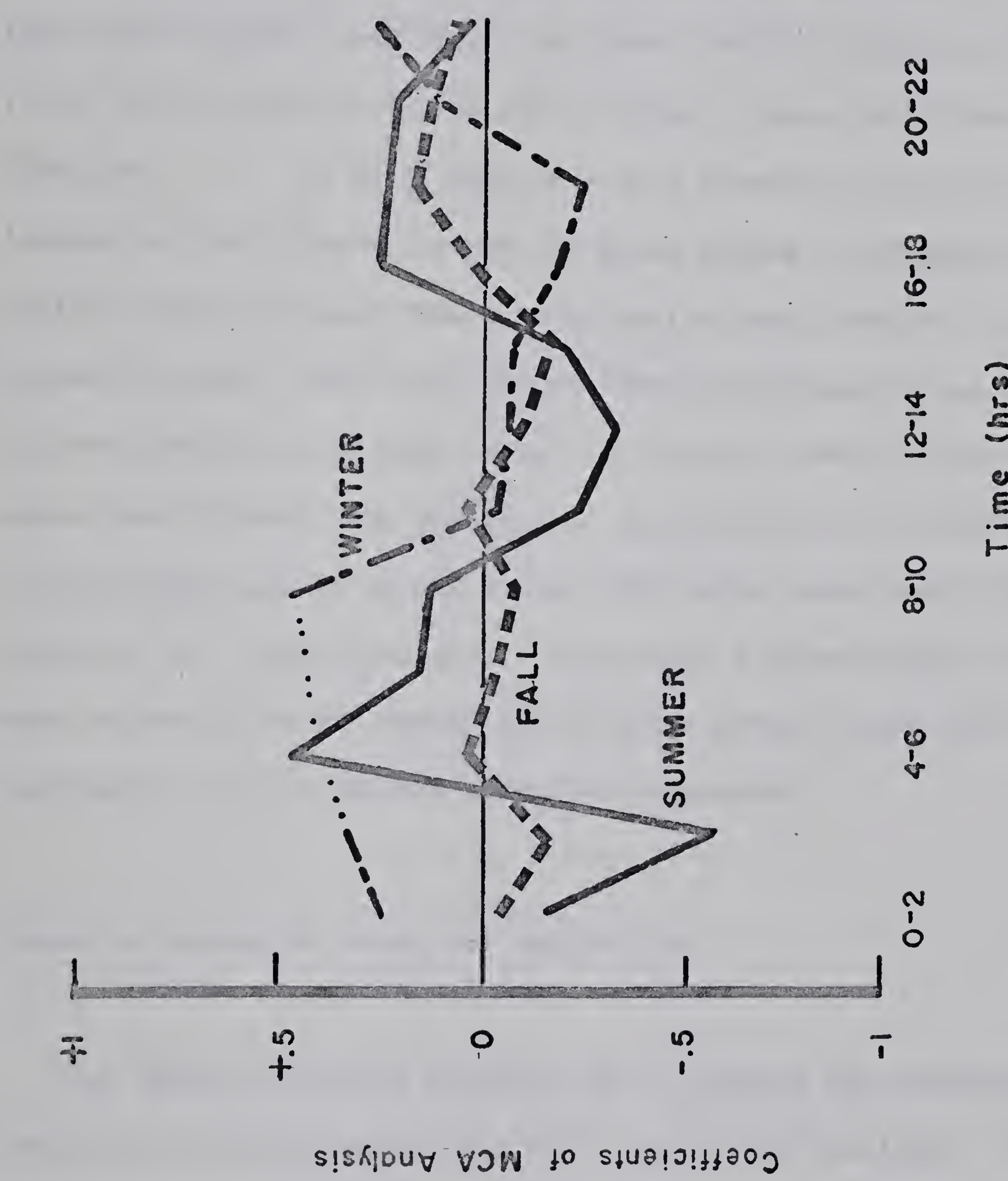
was the best in fall (Table 14).

Response profiles (Figure 5, Appendix 4) indicated that marten had a bimodal activity pattern in summer. The two periods of activity were from 0400 to 1000 hours and 1800 to 2400 hours. Sunrise occurred between 0230 and 0500 hours, and sunset between 1900 and 2330 hours. Marten were least active during the brightest and darkest periods of the day. Fall activity was less well defined. The period of greatest activity was from 1800 to 2400 hours. Sunrise occurred between 0500 and 0700 hours, and sunset between 1730 and 1900 hours. The increased number of overcast days and the small number of marten in the sample (two) may have biased the data during that season.

The winter radio-tracking sample was mainly from the day-time period because the colder night temperatures increased working difficulties and tended to render the radio equipment inoperative. Marten were active from at least 1000 to 1200 hours and 2200 to 0400 hours. Daylight hours were short; sunrise occurred between 0700 and 0930 hours, and sunset between 1430 and 1700 hours. It is noteworthy that marten were often live-trapped during the time period between the morning and evening trap rounds in winter months but never in the summer or fall. Poor hunting success (hunger) and higher winter energy requirements may be factors influencing marten activity rhythms.

Weather appeared to have an influence on marten activity. Marten tended to be active on overcast or rainy days, and inactive on clear or snowy days. Because of low values, the bias towards

Figure 5. Seasonal activity patterns of marten.


Coefficients of MCA Analysis
+1
+.5
0
-.5
-1
WINTER
FALL
SUMMER
0-2
4-6
8-10
12-14
16-18
20-22
Time (hrs)

activity during rain is only slight. There was a varying interrelationship between the amount of cloud cover and the time of day; clear sky at night had less influence on activity than clear sky during the day.

The habitat predictor is more difficult to interpret, and is the least valuable predictor. In summer, marten were more likely to be active when located in white spruce - aspen and black spruce - sphagnum. In fall, they were more likely to be active when located in jack pine - juniper and black spruce - sphagnum. In winter, they were more likely to be active when located in black spruce - lichen. This may indicate that marten spent less time in these habitats and were travelling through them to other areas when located. The presence of suitable dens or resting sites in other habitats my be one reason why marten were more likely to be inactive in these habitats. Marten dens located during the study were primarily in the dense, mature white spruce stands below the escarpment, or in crèvices along the escarpment.

Impact of Marten on Microtine Populations

The impact of marten predation on *C. gapperi* was estimated for the years in which marten food habits data were available. Seasonal population estimates for *C. gapperi* were based on Fuller (1977). Overwintering populations normally decline by 40 to 50 percent (Fuller 1977). Overwintered adults continue to decline in number after May and it is not until young of the first litter emerge in late June that population densities stabilize and slowly increase.

Only in late August do population densities increase rapidly. Crude densities were reduced by a factor of 2.5 in order to estimate numbers per ha (Fuller 1977). Then an estimate of *C. gapperi* numbers was derived for the total study area (Table 15). The exclusion of a portion of very open jack pine - juniper, not used by marten (More, unpublished data), enabled some correction for the bias that the entire study area contained habitats for optimum numbers of *C. gapperi*.

The impact of marten predation on *C. gapperi* (prey removed in proportion to prey numbers) was usually low (Table 15) and in years of average vole densities, only a minimal impact was evident. However, in 1974, *C. gapperi* densities rose substantially. Marten impact was higher than usual in the winter 1974-75 and, particularly, spring, 1975. Marten predation remained high until the following summer. Despite that pressure, *C. gapperi* densities rose to normal levels by August 1975 (Figure 5). Marten predation may have increased the depth of the low of the fluctuation in *C. gapperi*, but did not delay the increase phase. Misdating of scats and incorrect estimates of marten days on the study area could result in either overestimation or underestimation of voles consumed in any season.

It was not possible to determine if one sex was more vulnerable to predation than the other. However, as males move greater distances than females, and as their activity periods are slightly larger (McPhee 1977), it is possible that male voles were more available to marten.

Table 15. Impact of marten predation on *C. gapperi* on Heart Lake study area from 1973 to 1975.

Season	Year	Population Estimate* of *C. gapperi* (per 2000 ha)	Estimated Number of *C. gapperi* Consumed by Marten	Reduction of *C. gapperi* by Marten (%)
Summer	1973	6 000	602	10
Fall	1973	10 000	765	8
Winter	1973/74	8 500	1 412	17
Spring	1974	7 000	328	5
Summer	1974	15 000	1 630	11
Fall	1974	24 000	777	3
Winter	1974/75	12 300	2 682	22
Spring	1975	600	477	80
Summer	1975	5 300	477	9

* Population estimates after Fuller (1977).

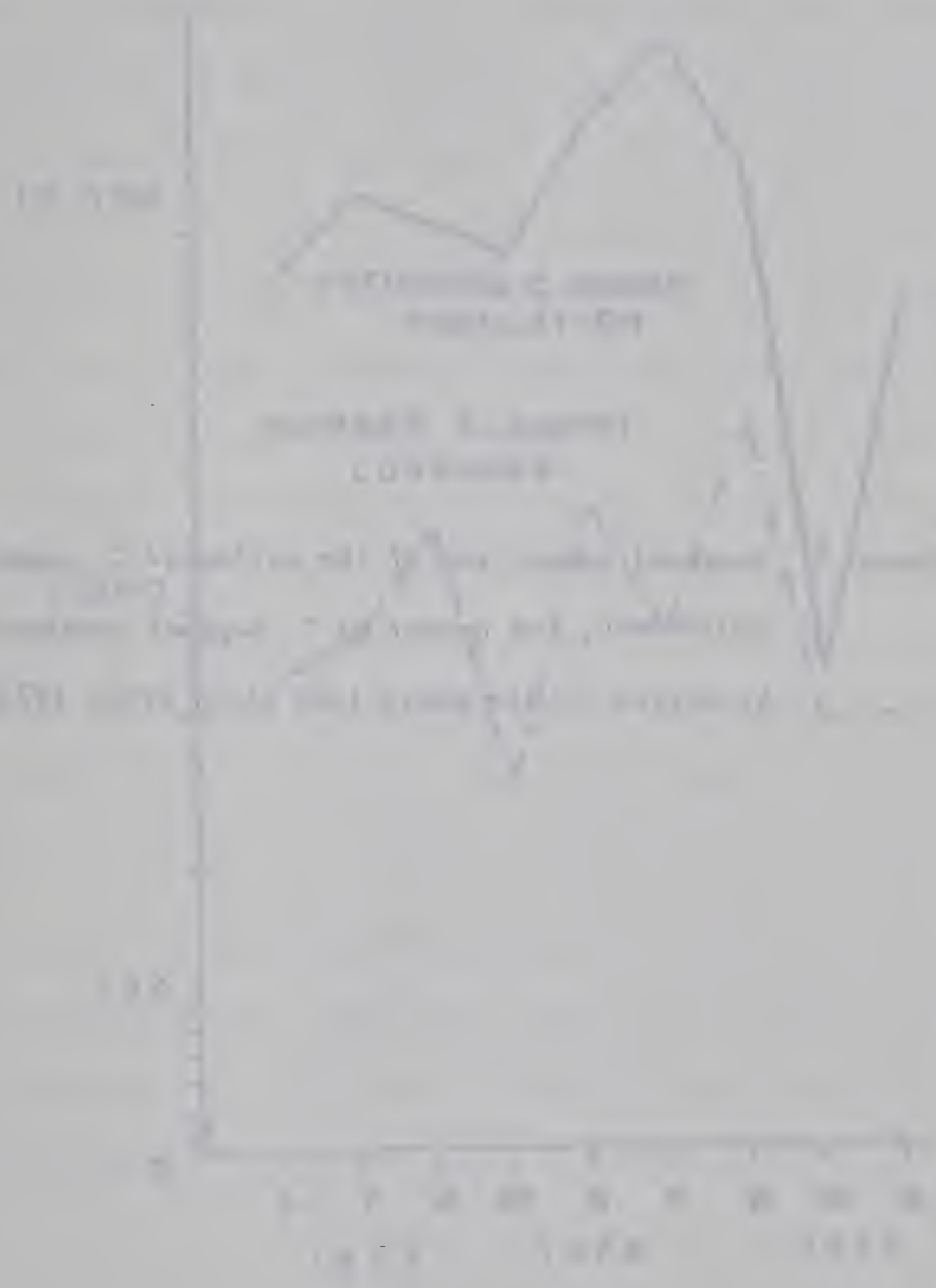
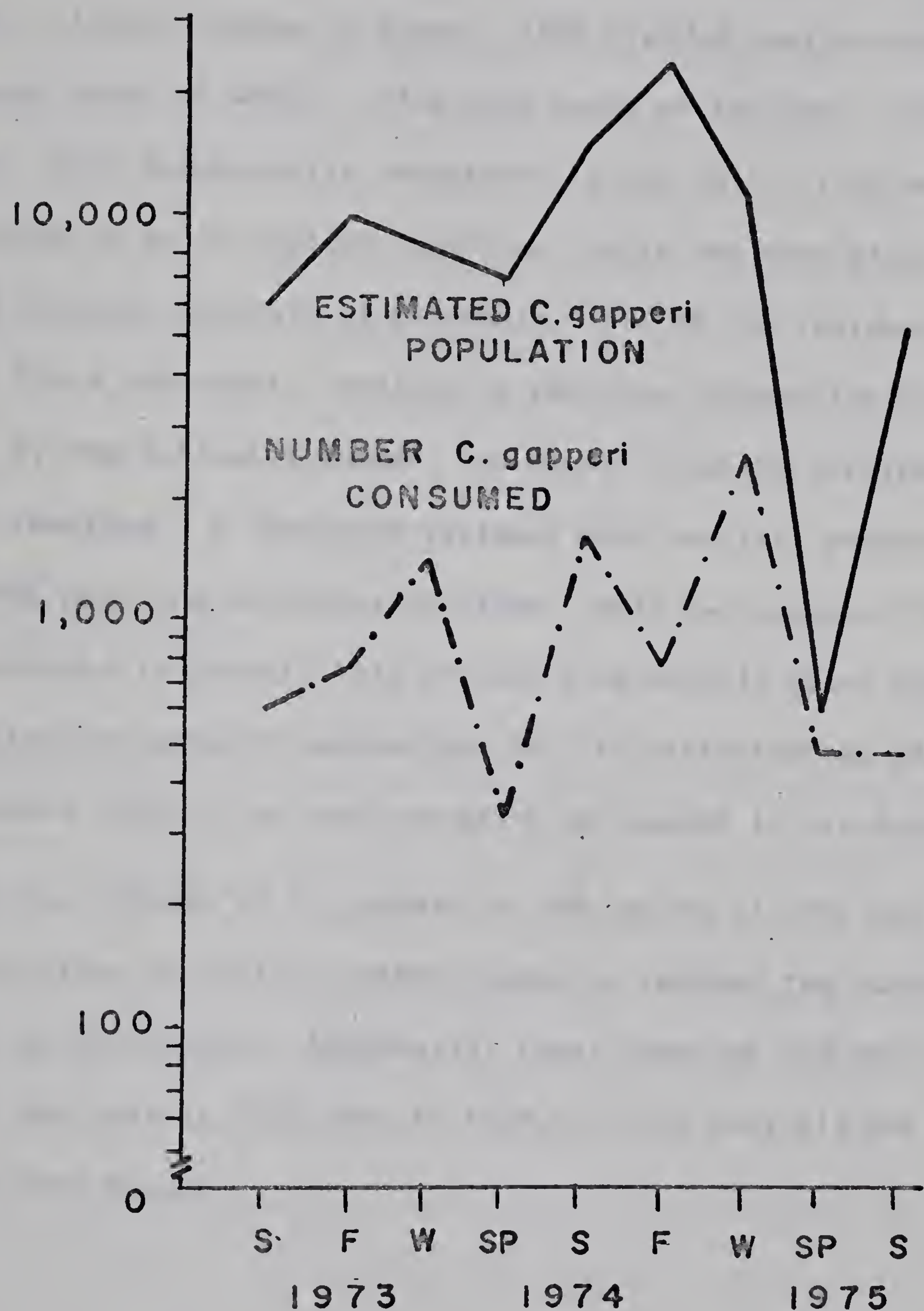


Figure 6. Seasonal comparison of the estimated *C. gapperi* population and , the number of *C. gapperi* consumed by marten in the Heart Lake study area, 1973-75.



10,000
1,000
100
0
ESTIMATED C. gapperi POPULATION
NUMBER C. gapperi CONSUMED
S F W SP S F W SP S
1973 1974 1975

Numerical Response of Marten

Data on changes in marten numbers in the study area were limited but will be mentioned because of the extreme fluctuations in small mammals. Live-trapping in August, 1974 yielded twelve marten on the study area of which, five were young of the year. Only two of the latter were subsequently recaptured in the fall. Four were considered to be in healthy condition, while one died after its second capture, possibly of pneumonia. All of the resident marten, except for a sub-adult, remained in the area through the winter of 1974. By the following summer, few adults from the previous summer remained. A long-term resident male was last observed in May, 1975 near the Biological Station. Only two young of the year were captured in August, 1975 and one died shortly after capture. The latter was grossly underweight for its estimated age (Brassard and Bernard 1939). One new sub-adult was caught in mid-August.

The low numbers of *C. gapperi* in the spring of 1975 may have induced marten to shift to other ranges or reduced the survivability of the marten. Apparently, fewer young of the year were born in the area in 1975 than in 1974, or else they did not survive into August.

DISCUSSION

Marten have been studied over a wide geographic range in North America. Certain similarities in food habits, habitats used, and activity patterns are apparent among those populations. Several facets of marten ecology were examined in this study. The results indicate that two ecological spacing mechanisms (time and space) are responsible for the similarities, particularly in food selection, despite differences in the prey bases and the factors affecting the ecological availability of the prey in the various studies.

Food Habits of Marten

Although marten food habits have been studied over much of the species' range in North America, no detailed comparison of prey utilization is possible. First, the occurrence of prey species and vegetation varies geographically (Iurgenson 1951). Second, there are differences in techniques between studies including: the timing of the collection of food data, the level of prey identification, the methods of calculation of occurrence of prey items, and the knowledge of prey densities. In addition, the wide variation in climate between study areas and between years of study affects the availability of prey and the prey densities.

Mammals are the major component of marten diet in all studies,

but the frequency of occurrence of the component items varies both seasonally and annually. Microtines are the principal food items; both *Clethrionomys* spp. (Cowan and Mackay 1950, Lensink et al. 1955, Quick 1955, Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Clark and Campbell 1977), and *Microtus* spp. (Murie 1961, Francis and Stephenson 1972, Douglass, R.J., L. Fisher and M. Mair, unpublished manuscript) have been reported as the major prey. The relative importance of each group is dependent on the habitats in the study areas, and the population densities of the various species present. *L. americanus* or *T. hudsonicus* may be important locally (Quick 1955) or seasonally (Marshall 1946, 1951), but, in general, these two species are low in occurrence in marten diet. Many other foods are eaten; insects, birds, and fruits are taken during the seasons in which they are most abundant and accessible. However, only a few of those foods occur in significant amounts, and rarely do such items supply a consistent food source.

Several studies have reported a low occurrence of *P. maniculatus* in marten diet despite an abundance of *P. maniculatus* in snap-trap samples (Cowan and Mackay 1950, Marshall 1951, Quick 1955, Weckwerth and Hawley 1962, Francis and Stephenson 1972, Koehler and Hornocker 1977, Clark and Campbell 1977). In the same studies, *Microtus* spp. were rated as low in abundance, based on snap-trap samples, and yet were common food items. This apparent contradiction has led most investigators to assume a selection or preference for *Microtus* spp. and an avoidance of *P. maniculatus*. However, this conclusion may oversimplify the mechanisms which

may alter the ecological availability of prey to marten.

Little evidence was found in this study to indicate marten had a selective preference for the prey found most frequently in scats (*C. gapperi*) over the prey found least frequently (*P. maniculatus*). It is possible that preference for an item reflects either the energy 'reward' or the acquisition of other nutrients from particular prey items. Published studies reveal some caloric difference between species of small mammals preyed upon by marten. Mean caloric values per gram of biomass for *P. maniculatus*, *C. gapperi*, and *M. pennsylvanicus* were 1.85, 1.69 (Bergeron 1976), and 1.4 Kcal/g (Golley 1961), respectively. However, *M. pennsylvanicus* would be the most rewarding animal to prey upon when its greater adult weight is considered. Therefore, some advantage does accrue when marten prey upon voles instead of *P. maniculatus*.

Habitat

Mature, mixed coniferous stands are the preferred habitats of marten and sable (*Martes zibellina*) over a large geographic range (Marshall 1951, De Vos 1952, Hawley 1955, Francis and Stephenson 1972, Grakov 1972, Wooley 1974, Koehler et al. 1975, Koehler and Hornocker 1977, Clark and Campbell 1977, Douglass, R.J., L. Fisher and M. Mair, unpublished manuscript, Mech and Rogers 1977). Less favored habitats reported include open black spruce bogs, and hardwood dominated stands (De Vos 1952, Francis and Stephenson 1972, Grakov 1972, Wooley 1974). The results of the

present study agree with the habitat observations in other studies. Associations of moderate to heavy stand density dominated by white spruce were the most used habitats. Some use of deciduous and black spruce dominated habitats was observed. Very open sites, wet or dry, were not used in proportion to the availability of such habitats on the study area.

The data suggest two reasons for the observed frequency of use by marten of certain habitats. Highly used habitats generally had higher numbers of small mammals (Table 8), and other prey such as *L. americanus* and *T. hudsonicus* (pers. obs.). Numbers of *C. gapperi*, the principal food, were highest in those habitats (Table 8, Appendix 3). There was less use by marten of habitats used by *P. maniculatus*; this may be a partial reason why that species forms a small part of the marten diet. *M. pennsylvanicus* were high in occurrence in marten diet despite almost no recorded use of the optimum habitats of this prey. However, it was not possible to take into account the numerous small, grassy openings in forest stands of moderate to heavy canopy closure in which *M. pennsylvanicus* may be locally abundant. Moreover, the method used to determine the population densities of *M. pennsylvanicus* underestimated the actual numbers that occur in the black spruce associations (D. Doyle, unpublished data). As black spruce - lichen habitats with low *C. gapperi* densities were used by marten, it seems likely that the marten were searching for *M. pennsylvanicus*. In addition, *M. pennsylvanicus* have been shown to shift into adjacent forest types during highs in their population and in winter (Turner et al. 1975).

The second reason for high use by marten of white spruce dominated habitats is the availability of maternal and day den sites (Mech and Rogers 1977). One maternal den found in a dense white spruce stand consisted of 10-15 openings dug at the base of tall trees or in the deeper soil banked along the base of a bedrock outcrop, below the escarpment. Signs around the area indicated that it had been used over a long period of time. Large squirrel middens found in similar habitats and brush piles may serve as day dens.

Some variation in use of habitats by marten may be explained by the population densities of the prey species. In years of low prey densities, habitats optimum for major prey species may be crucial to a predator. Ryszkowski et al. (1973) reported carnivore concentrations in small areas of high prey density within larger areas of generally low density. In years of high prey numbers, overflow into marginal habitats, where prey are probably insecure, could affect marten population distribution and numbers in either of two ways. First, resident marten may continue to utilize only a few prime prey habitats within their home range, thus permitting non-resident marten to use the normally less productive habitats successfully while the over-flow of prey lasts. The alternative reason is that high populations of *C. gapperi* may reduce the need of resident marten to be highly selective in the use of habitats, particularly of hardwood stands; and resident marten may be more tolerant of transients on their home ranges. Either strategy results in a higher population density of marten per unit of area during a period of prey abundance.

Activity

Marten tend to be inactive during the day in summer (Marshall 1951, Remington 1952, Clark 1977), and increase the amount of daytime activity in winter (Hawley 1955, Herman and Fuller 1976). Marten activity patterns in the present study were similar. Marten had bimodal activity periods in the early morning and evening in summer. These periods of activity were modified in fall and winter. Marten were seldom active between mid-morning and late afternoon in summer, but were active during the morning in winter. These changes in the circadian rhythm of marten may be attributable to changes in climate, variations in the length of day, colder temperatures, and snow accumulation. In the same way, diel activity patterns may vary with short-term environmental changes, particularly daily weather patterns. Other causes may be poor hunting success or greater energy demands due to low temperatures (Clem 1977). One explanation for the alterations in circadian and daily activity rhythms is that the quality of vision of pine marten is best suited for dim light conditions rather than bright light or darkness (Kavanau and Ramos 1975). Thus, marten may remain active at mid-day during summer if it is cloudy, while on sunny days marten would remain in a day den.

One way for a predator to increase the probability of encountering prey is to be active during the same time period as their prey. Changes in activity patterns of prey, either seasonally or short term, may, therefore, indirectly affect the behavior and activity of marten. *C. gapperi* have a polyphasic

diel activity pattern with bimodal peaks in activity prior to sunrise and following sunset during summer, fall and early winter, with a unimodal afternoon peak in mid-winter (Stebbins 1971, Friesen 1972, Herman 1975, McPhee 1977). This activity pattern most closely resembles that of marten. *P. maniculatus* has a different diel rhythm; essentially confined to a unimodal nocturnal peak of activity in summer and bimodal nocturnal peaks in winter (Stebbins 1971, Friesen 1972). The activity pattern of *M. pennsylvanicus* (in Michigan) is somewhat intermediate in the amount of overlap with marten activity; the daily activity period in summer is depressed at night from 0100 to 0500 hours (Ambrose 1973). Other species are equally unavailable based on the criterion of overlap in the time of activity. *T. hudsonicus* is strictly diurnal in summer and winter (Zirul 1970), while the summer activity of *L. americanus* occurs mainly from 2030 to 0130 hours (Keith 1964). That *T. hudsonicus* is so high in occurrence in summer scats may indicate a degree of vulnerability while they are in middens.

Certain other behavioral characteristics may increase or decrease the availability of small mammals as prey. Vole species are active all year, and some construct runways and above-ground nests in winter. *P. maniculatus*, however, often enters a state of torpor lasting two or three days at a time in winter (Stebbins 1971, Friesen 1972). *E. minimus* hibernates from October to March (Smith 1971). *T. hudsonicus* reduces its activity in fall and winter and retreats during freezing weather (-29°C) to intranivean movement and sheltering in middens (Zirul 1970).

Predator Strategy

Marten generally are classified as opportunistic hunters because of the diversity of foods consumed. It is a major finding of the present study that marten, in fact, have a definite hunting strategy; that of maximizing the degree of overlap, both temporally and spatially, with certain prey that are available year round and that are abundant in a number of habitats. The following observations are cited in support of this conclusion:

(a) in spite of the diversity of food items consumed (including 11 mammal species; four orders of birds; three orders of insects; and fruits of 12 plant species (Appendix 1)), relatively few species contribute significantly to the diet of marten based on frequency of occurrence (Appendix 1) or relative biomass (Table 3);

(b) activity periods of pine marten coincide temporally with those of the major prey;

(c) preferred habitats of marten are those containing the principal food species in the greatest quantities;

(d) alternate prey are used mainly during periods of decline or low numbers of the major prey (*C. gapperi*), or during periods of environmental stress (winter); and

(e) high population densities of a potential prey are not sufficient to result in a corresponding high use of that species as a major prey. Although *P. maniculatus* populations were high during the study, the habitats preferred by *P. maniculatus* overlapped only partially with the habitats preferred by pine marten, and the activity periods of each species overlapped minimally.

Predator - Prey Interrelationships

A number of studies suggest that predators may contribute significantly to declines in populations of small mammals (Pearson 1966, 1971, Maher 1967, Maclean et al. 1974, Fitzgerald 1977) and lagomorphs (Keith 1974). Other studies note that the heaviest predator impact occurs during the decline phase of lagomorphs (Wagner and Stoddart 1972) and small mammals (Ryszkowski et al. 1971, Ryszkowski et al. 1973). While predation does not initiate the decline in prey, heavy predation during the decline phase is thought to cause prey numbers to be depressed to lower levels than would result without this pressure, and to delay their recovery (for a review, see Erlinge 1975a).

In the present study, the impact of marten predation on *C. gapperi* was minimal during the increase phase of *C. gapperi*. Maximum impact occurred during the decline of *C. gapperi*; however, the decline itself was caused by unknown factors (Fuller 1977). There is no support for the suggestion that marten predation caused the *C. gapperi* population to decline to extremely low

numbers. Nor did marten predation, combined with predation of the short-tailed weasel (*Mustela erminea*), the other major predator of *C. gapperi* on the study area (D.R. Wooley, pers. comm.), delay the subsequent increase in *C. gapperi* numbers (Fuller 1977). Once breeding began, *C. gapperi* numbers increased despite all sources of predation. Ryszkowski et al. (1973), Fuller et al. (1975) and Boonstra (1977) also noted that small mammals increased to either normal or high densities during the breeding season following declines associated with significant predation.

Only one other mammalian predator, the short-tailed weasel, occurred in significant numbers on the Heart Lake study area (pers. obs.). Even highly mobile predators such as raptors, which may show an extreme functional response (Schnell 1968) or numerical response (Rusch et al. 1972, McInvaille and Keith 1974), were rare in both years. The low variety of predators may account for the minimal impact of predation on *C. gapperi* in the present study. In addition, other studies reported on extremely specialized predators (weasels and feral house cats (*Felis cattus*)) preying on highly vulnerable prey (*Microtus* spp. or lemmings) (Pearson 1971, Fitzgerald 1977).

The numerical response of marten in the Heart Lake Study was consistent with the response reported in Montana by Hawley and Newby (1957), and Weckwerth and Hawley (1962); poor physical condition of females, reduced production of young, and high juvenile dispersal occurred at the time of a decline in small mammal numbers. The amount of alternative prey captured was

insufficient to support the marten population. Possibly certain segments of the marten population were unable to prey upon larger prey with adequate success to maintain themselves. Apparently, the most vulnerable members of the population were young marten and females. Lack of success, then, may be directly related to the smaller size of those marten.

It is likely that small mammals are more important to marten population dynamics than previously believed, particularly in northern regions where the diversity of alternative prey is less than in the southern portions of the pine marten's range. A similar result was reported for lynx after the decline of a snowshore hare population (Brand et al. 1976). Keith (1974) hypothesized that a decrease of predator populations is a necessary condition to permit hares to increase. Perhaps the reduction of the marten population frees the *C. gapperi* population from extended periods of heavy predator pressure.

Under normal conditions, predation on small mammals alone is almost sufficient to furnish the minimum daily food requirements of marten. Of an estimated 401 050 g of digestible biomass required by marten on the study area (Table 7), 94 percent were provided by small mammals, of which *C. gapperi* supplied almost two-thirds and *M. pennsylvanicus* almost one-third (Table 6). The remainder was obtained through predation on other species.

Increased population densities of *C. gapperi* resulted in a corresponding increase in the use of that prey because of a direct rise in encounters between marten and its principal prey. In years

of extremely low *C. gapperi* numbers, alternative foods have to make up a larger portion of the marten diet. If alternative prey cannot be caught in relation to their abundance, either because of an ecological spacing mechanism or the inability of marten to catch certain prey, the effect on the marten is severe.

More *L. americanus*, *T. hudsonicus* and grouse were present in scats in years other than the year of the peak in *C. gapperi* numbers (Appendix 1). A slight increase in the predation rate on larger species results in a higher return of biomass to the predator than an increase on smaller species (McInvaille and Keith 1974). However, such large prey were probably more available to adult males than to juveniles and small females (Erlinge 1975b). Because of the reduced availability of large prey to some marten, it is debatable whether marten numbers would have been maintained even if large prey had been more numerous.

Rosenzweig (1966) suggested that specialization of as large a predator as marten on small mammals may be an adaptation to reduce competition with fisher. Clem (1977) reported a short-term overlap in the diet of the two species in mid-winter only. The physical size of the pine marten, therefore, may be related to two factors. Because males are larger than females and juveniles, they can take larger prey. This removes some of the competition between males and other segments of the marten population. Secondly, marten are able to meet most of their food requirements by preying on small mammals. Their size enables them to kill, at least occasionally, other prey during the periods when microtines are less abundant.

CONCLUSIONS

The most important factor in food selection in pine marten is the ecological availability of prey, and the corresponding factors which result in an increased susceptibility and vulnerability of prey to marten predation. In short, marten food selection is based on two ecological spacing mechanisms - the overlap of activity periods and habitats of the predator and potential prey.

In the Heart Lake area, the species most available to marten, based on the criteria of temporal and spatial overlap, is *C. gapperi*, the principal food item in the marten diet. *M. pennsylvanicus* had the next greatest temporal overlap, but reduced spatial overlap. It was consistently important in the diet of marten throughout the study. The low occurrence of *P. maniculatus* in marten diet apparently is the result of a reduced spatial and temporal overlap with marten, rather than an avoidance or dislike of *P. maniculatus* by marten.

The present study supports the conclusion of Rosenzweig (1966) that pine marten tend to be specialists on small mammals despite the fact that marten are large in relation to the size of their prey. Marten met their minimum food requirements almost totally from small mammals when the microtine populations were normal or high. The remaining food requirements were obtained from other sources. Pine marten tended to become more diverse in their food selection as microtine populations declined as predicted by Emlen (1968). Marten populations dropped after a decline in small mammal

numbers indicating that marten were not sufficiently able to use the total available prey base in the area.

Pine marten were not a major factor in microtine fluctuations despite apparent heavy predation during the most vulnerable phase of the *C. gapperi* fluctuation - the decline phase. The results do not support the hypothesis that predation during and following a microtine decline is the cause of the timing and amplitude of the microtine cycle (Pearson 1971). It is possible that the population density of *C. gapperi* was lowered below what the population density would have been had marten predation been absent, but no evidence is available to show that the decrease phase of *C. gapperi* was lengthened as a result of marten predation.

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Appendix 1. Percentage of occurrence* of food items in marten scats from Heart Lake, 1973-75. Sample size is in parentheses.

FOOD ITEMS	1973 Summer (25)	1973 Fall (6)	1974 Winter (47)	1974 Spring (51)	1974 Summer (131)	1974 Fall (86)	1975 Winter (110)	1975 Spring (20)	1975 Summer (25)	1973-75 Total (501)
MAMMAL										
Clethrionomys gapperi	44	67	36	23	48	63	61	70	28	50
Microtus pennsylvanicus	44		23	18	22	16	10	15	16	18
Phenacomys intermedius			2		1		2		4	1
Synaptomys borealis			2	8	3	2	4		8	3
Peromyscus maniculatus			2	10	7	2	3		8	4
Cricetidae UI	12	17	30	35	21	21	23	15	25	23
Tamiasciurus hudsonicus	4		4	2	9	3	7	10	12	6
Glaucomys sabrinus			2							Tr
Lepus americanus			28	6	3	2	1	10		5

FOOD ITEMS	1973 Summer (25)	1973 Fall (6)	1974 Winter (47)	1974 Spring (51)	1974 Summer (131)	1974 Fall (86)	1975 Winter (110)	1975 Spring (20)	1975 Summer (25)	1973-75 Total (501)
MAMMAL (cont'd)										
Sorex cinereus	8		2	2	1	1	1	5	4	2
Sorex arcticus	4						2			1
Microsorex hoyi					1	1	6			2
Soricidae UI			2			2	3			1
Mammal UI							1		4	Tr
AVES										
Galliformes	28		4	19	7	1	4	5	12	7
Passeriformes	4		15	10	6	1	5	5	4	6
Falconiformes					1	1	1		4	1
Charadriiformes							1	5		Tr
Bird UI	12	33	2	6	4		2			3
Eggshell	12		2				2		4	2

FOOD ITEMS	1973 Summer	1973 Fall	1974 Winter	1974 Spring	1974 Summer	1974 Fall	1975 Winter	1975 Spring	1975 Summer	1973-75 Total
	(25)	(6)	(47)	(51)	(131)	(86)	(110)	(20)	(25)	(501)
INSECTA										
Coleoptera	4									Tr
Hymenoptera	12				24	2			36	12
Diptera	4				1					Tr
Unknown				4	4		1			2
MOLLUSCA	4				1					Tr
VEGETATION										
Arctostaphylos uva-ursi	16	67	6	20	5	5	2		4	7
Arctostaphylos rubra				2		2				1
Empetrum nigrum	4				2	10	4	10	28	5
Vaccinium vitis-idaea	16	17	2	16	4	10	4	5	4	7
Rubus strigosus					1	1	1		20	2
Rubus oxyacanthoides							1			Tr
Rosa acicularis	4	17	2		1	19	16			8

FOOD ITEMS	1973 Summer	1973 Fall	1974 Winter	1974 Spring	1974 Summer	1974 Fall	1975 Winter	1975 Spring	1975 Summer	1973-75 Total
	(25)	(6)	(47)	(51)	(131)	(86)	(110)	(20)	(25)	(501)
VEGETATION (cont'd)										
Viburnum edule					1	1				Tr
Cornus canadensis					1					Tr
Shepherdia canadensis				2	2	1	1			1
Juniperus communis						2	2	5	12	2
Geocaulon lividum			2							Tr
Grasses	8		6	8	3		3	5		4
Needles				8	1				4	1
Vegetation UI		17	8	6	5	2	2			4

* Based on presence or absence of item only.

Abbreviations: UI = Unidentified
Tr = Trace

Appendix 2. Response profiles: coefficients of MCA model of marten habitat use.

PREDICTOR VARIABLE and LEVELS**		Summer	Fall	Winter
1. HABITAT AT POINT LOCATIONS				
Black Spruce/Sphagnum	a	-0.424	-0.206	-0.027*
	b	-0.116	-0.269	-0.034
	c	--	--	--
Black Spruce/Lichen	c	0.177	-0.051*	0.035*
	d	-0.192	-0.305	-0.236
	e	--	--	--
White Spruce/Black Spruce	a	--	--	--
	b	-0.500	-0.005*	-0.045*
	c	0.233	0.169	0.527
	e	--	--	--
White Spruce/Aspen	b	--	--	--
	c	0.120	0.296	0.325
	d	0.245	0.299	-0.387
	e	-0.137	-0.237	-0.084*
White Spruce/Jack Pine	a	-0.208	-0.011	-0.214
	b	-0.312	-0.273	-0.283
	c	-0.033*	-0.087*	0.046*
	d	0.122	-0.016*	-0.139
	e	0.135	0.082*	0.127
Aspen	a	--	--	--
	b	--	--	--
	c	--	--	--
	e	0.219	0.276	-0.398
Jack Pine/Juniper	a	-0.246	-0.289	-0.331
	b	-0.250	-0.255	-0.061*
	c	-0.564	-0.806	0.111
	d	--	--	--
	e	-0.311	-0.242	0.094

PREDICTOR VARIABLE and LEVELS**		Summer	Fall	Winter
1. HABITAT AT POINT LOCATIONS (cont'd)				
Water		-0.030*	-0.142	-0.179
Rock		--	--	--
2. FIRST CLOSEST HABITAT				
Black Spruce/Sphagnum	a	-0.213	-0.145	0.042*
	b	-0.075*	-0.010*	-0.218
	c	0.484	0.370	0.042*
Black Spruce/Lichen	c	0.086*	-0.104	-0.017*
	d	-0.367	-0.253	-0.187
	e	-0.444	0.167	0.506
White Spruce/Black Spruce	a	-0.688	-0.323	-0.282
	b	-0.373	0.002*	-0.145
	c	-0.516	-0.151	-0.212
	d	0.031*	-0.078*	0.096
	e	--	--	--
White Spruce/Aspen	b	--	--	--
	c	0.170	0.182	0.263
	d	0.270	0.013*	0.263
	e	0.285	0.197	0.004*
White Spruce/Jack Pine	a	-0.372	-0.186	-0.043*
	b	0.046*	-0.306	0.046*
	c	0.059*	0.224	0.114
	d	0.143	-0.083*	0.208
	e	0.125	0.054*	0.124
Aspen	a	--	0.184	--
	b	--	0.343	--
	c	--	--	--
	e	0.216	0.177	-0.223
Jack Pine/Juniper	a	-0.457	-0.292	-0.566
	b	-0.147	-0.110	0.020*
	c	-0.473	-0.480	-0.199

PREDICTOR VARIABLE and LEVELS**		Summer	Fall	Winter
2. FIRST CLOSEST HABITAT (cont'd)				
Jack Pine/Juniper	d	--	--	--
	e	-0.231	-0.618	-0.813
Water		0.031*	-0.187	-0.216
Rock		0.490	--	--
3. SECOND CLOSEST HABITAT				
Black Spruce/Sphagnum	a	-0.178	-0.250	-0.096
	b	-0.259	-0.397	-0.145
	c	0.306	0.010*	-0.388
Black Spruce/Lichen	c	-0.082*	-0.056*	-0.226
	d	0.149	0.036*	0.023*
	e	0.653	0.503	0.372
White Spruce/Black Spruce	a	0.108	-0.041*	-0.381
	b	-0.486	0.392	0.412
	c	0.360	0.230	0.452
	d	-0.441	-0.033*	-0.054*
	e	-0.071	-0.236	-0.070*
White Spruce/Aspen	b	-0.088*	-0.027*	-0.427
	c	0.117	-0.042*	0.262
	d	-0.152	0.041*	-0.138
	e	-0.015*	0.211	0.006*
White Spruce/Jack Pine	a	--	--	--
	b	0.155	-0.342	-0.206
	c	0.177	0.334	0.252
	d	0.069*	0.013*	-0.128
	e	0.009*	0.026*	-0.486
Aspen	a	--	0.688	--
	b	--	0.053*	--
	c	--	--	--
	e	0.000	--	-0.002*

PREDICTOR VARIABLE and LEVELS**		Summer	Fall	Winter
3. SECOND CLOSEST HABITAT (cont'd)				
Jack Pine/Juniper	a	0.014*	-0.156	-0.477
	b	0.044*	-0.175	0.051*
	c	0.210	0.329	-0.155
	d	-0.213	-0.110	-0.476
	e	0.583	--	0.526
Water		-0.280	-0.233	-0.207
Rock		--	--	--

* Coefficient value approaches zero indicating minimal difference between groups.

** Canopy Density (Percent): a = 0-20 b = 21-40 c = 41-60 d = 61-80 e = 81-100

Appendix 3. Response profiles: coefficients of MCA model of small mammal prevalence.

PREDICTOR VARIABLE and LEVELS	Summer	Fall	Winter
1. PREVALENCE OF ALL SMALL MAMMALS AT POINT LOCATIONS			
Absent	-0.253	-0.216	-0.082*
Rare	-0.199	-0.197	-0.056*
Low	-0.152	-0.100	-0.025*
Moderate	0.062*	-0.045*	0.068*
High	0.149	0.271	0.152
2. PREVALENCE OF *C. GAPPERI* AT POINT LOCATIONS			
Absent	-0.211	-0.272	-0.272
Rare	-0.247	-0.196	-0.060*
Low	-0.047*	-0.034*	-0.047*
Moderate	0.067*	-0.034*	0.094
High	0.192	0.311	0.227
3. PREVALENCE OF *P. MANICULATUS* AT POINT LOCATIONS			
Absent	-0.151	-0.097	-0.060*
Rare	-0.159	-0.182	-0.134
Low	-0.052*	-0.166	0.016*
Moderate	0.115	0.128	0.050*
High	--	--	--
4. PREVALENCE OF *M. PENNSYLVANICUS* AT POINT LOCATIONS			
Absent	0.037*	0.058*	0.038*
Rare	-0.022*	-0.196	-0.007*
Low	-0.134	-0.198	-0.102
Moderate	-0.107	-0.004*	-0.127
High	--	--	--

* Coefficient value approaches zero indicating minimal difference between groups.

Appendix 4. Response profiles: coefficients of MCA model of marten activity.

PREDICTOR VARIABLE and LEVELS	Summer	Fall	Winter
1. TIME OF DAY			
00 01 - 02 00	-0.148	-0.042*	0.254
02 01 - 04 00	-0.597	-0.161	0.312
04 01 - 06 00	0.489	0.046*	--
06 01 - 08 00	0.167	-0.039*	--
08 01 - 10 00	0.129	-0.086*	0.486
10 01 - 12 00	-0.235	0.019*	-0.029*
12 01 - 14 00	-0.317	-0.100	-0.084*
14 01 - 16 00	-0.200	-0.145	-0.096
16 01 - 18 00	0.267	0.037*	-0.192
18 01 - 20 00	0.232	0.190	-0.213
20 01 - 22 00	0.218	0.136	0.101
22 01 - 24 00	0.019*	0.066	0.291
2. WEATHER			
Clear	-0.056*	-0.108	-0.044*
Overcast	0.128	0.140	0.174
Rain	0.035*	0.028*	--
Snow	--	-0.104	-0.203
3. HABITAT			
Black Spruce/Sphagnum	0.145	0.228	0.000
Black Spruce/Lichen	-0.193	--	0.210
White Spruce/Black Spruce	-0.229	-0.154	0.008*
White Spruce/Aspen	0.275	-0.108	-0.176
White Spruce/Jack Pine	-0.096	-0.027*	0.052*
Aspen	0.084*	0.031*	--
Jack Pine/Juniper	0.028*	0.451	-0.147

* Coefficient value approaches zero indicating minimal difference between groups.